QL
671
.I7
1950

HARVARD UNIVERSITY

VE RI
TAS

LIBRARY

OF THE

Museum of Comparative Zoölogy

MUS. COMP. ZOOL.
LIBRARY

HARVARD
UNIVERSITY

Aj-C

# PROCEEDINGS
# of the
# Xth International Ornithological Congress

*Uppsala June 1950*

MUS. COMP. ZOOL
LIBRARY
MAR 8 195
HARVARD
UNIVERSITY

PUBLISHED WITH THE AID OF GRANTS FROM THE
SWEDISH STATE, FROM THE UNITED NATIONS EDUCATIONAL, SCIENTIFIC
AND CULTURAL ORGANIZATION, AND FROM THE SMITHSONIAN INSTITUTION.
UNDER THE PATRONAGE OF THE INTERNATIONAL UNION
OF BIOLOGICAL SCIENCES.

UPPSALA · STOCKHOLM
ALMQVIST & WIKSELLS BOKTRYCKERI AB

# PROCEEDINGS
of the
# Xth International Ornithological Congress

388
37

# PROCEEDINGS
OF THE
# Xth INTERNATIONAL ORNITHOLOGICAL CONGRESS

*Uppsala June 1950*

UNDER THE PRESIDENCY OF
ALEXANDER WETMORE

*Edited by*
SVEN HÖRSTADIUS
GENERAL SECRETARY

Printed at *Almqvist & Wiksell* · *Uppsala 1951*

PUBLISHED WITH THE AID OF GRANTS FROM THE
SWEDISH STATE, THE UNITED NATIONS EDUCATIONAL, SCIENTIFIC
AND CULTURAL ORGANIZATION, AND THE SMITHSONIAN INSTITUTION,
WASHINGTON. UNDER THE PATRONAGE OF THE INTERNATIONAL
UNION OF BIOLOGICAL SCIENCES

MUS. COMP. ZOOL.
LIBRARY
MAR 8 1954
HARVARD
UNIVERSITY

*Almqvist & Wiksells*
BOKTRYCKERI AKTIEBOLAG
UPPSALA 1951

# Preface

The present Proceedings differ from previous ones through the presence of four synoptical papers on central domains in ornithology, which were presented in the program of the Congress at the request of the Executive Committee. These surveys, by Messrs. Drost, Lack, Mayr and Tinbergen, in addition to the presidential address, which also consists of a recapitulatory survey, as well as the introduction to Swedish Ornithology have been published without abridgement and with complete bibliographies. It has been possible to allow the authors of the remaining contributions, on the other hand, only limited space, as more detailed essays on account of the great number of contributors were out of the question for economic reasons, and as according to the editor's opinion the Proceedings of a Congress are not the place for extensive original papers. Many authors have, therefore, had to limit themselves to short reports and references to places for detailed publication. The editor is grateful to the authors for their appreciation of this difficulty.

The Executive Committee is extremely grateful to the Swedish Government, and to the United Nations' Educational, Scientific and Cultural Organization, as well as to the Smithsonian Institution for the financial support, which has rendered possible the publication of these Proceedings. We are also greatly indebted to Professor Arthur A. Allen, Ithaca, for his kind gift of the clichés for the coloured plate.

Manuscripts in English, German or French by authors who have not had the language in question as their mother tongue, have been scrutinized by native-born revisers. In addition Miss Phyllis Barclay-Smith, London, read the proofs for all contributions in English by authors not speaking English. The editor would like to express his hearty thanks for this valuable assistance, and also to the President, Dr. A. Wetmore, who has kindly checked the account of the Congress and the lists of members.

The editor has found no reason to encroach upon the authors' style of writing by introducing uniformity regarding the use of capital and lower case letters in the names of birds and in titles.

The material for this volume was available in the autumn of 1950. No manuscripts have been received from Dr. H. Johansen and Mr. W. Vogt. The editor regrets that the printing has taken such a long time.

Uppsala, November 1951

*Sven Hörstadius.*

# Contents

The Xth International Ornithological Congress . . . . . . . . . . . . . . . 13
  The Congress at Uppsala 10th—17th June 1950 . . . . . . . . . . . . . 13
  Excursions before and after the Congress . . . . . . . . . . . . . . . . 20
  Birds observed during the excursions . . . . . . . . . . . . . . . . . 28
  Programme . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 34
  List of Delegates . . . . . . . . . . . . . . . . . . . . . . . . . . . 42
  List of Members of the Congress . . . . . . . . . . . . . . . . . . . . 45

ALEXANDER WETMORE: Presidential Address. Recent Additions to our Knowledge of Prehistoric Birds 1933—1949 . . . . . . . . . . . . . . . . . . 51

SVEN HÖRSTADIUS: Introduction to Swedish Ornithology . . . . . . . . . . 75

## Evolution and Systematics

ERNST MAYR: Speciation in Birds. Progress Report on the Years 1938—1950 91
ERWIN STRESEMANN: Der Einfluss philosophischer Naturbetrachtung auf die ornithologische Systematik . . . . . . . . . . . . . . . . . . . . . . . 132
ELSA G. ALLEN: A Sixteenth Century Classification of Birds . . . . . . . . 139
ALESSANDRO GHIGI: Nomenclature in Guinea Fowls . . . . . . . . . . . . . 144
FINN SALOMONSEN: A Nomenclatorial Controversy: The Genus *Colymbus* Linnaeus 1758 . . . . . . . . . . . . . . . . . . . . . . . . . . . . 149
R. MEINERTZHAGEN: Desert Colouration . . . . . . . . . . . . . . . . . . 155
CHARLES VAURIE: Adaptive Differences between Two Sympatric Species of Nuthatches (*Sitta*) . . . . . . . . . . . . . . . . . . . . . . . . . 163
JAMES M. HARRISON: Some Phylogenetic Trends in *Garrulus glandarius* Linnaeus and *Dendrocopos major* (Linnaeus) . . . . . . . . . . . . . . . . 167
W. B. YAPP: Ecological Speciation in the Genus *Phylloscopus* . . . . . . . . 173
DEAN AMADON: Evolution of the Hawaiian Honeycreepers (Family *Drepanididae*) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 176
K. H. VOOUS: Distributional and Evolutionary History of the Kingfisher Genus *Ceyx* in Malaysia . . . . . . . . . . . . . . . . . . . . . . . . . . 177
DEAN AMADON: Madagascar's Pseudo-sunbird . . . . . . . . . . . . . . . . 184

Robert A. H. Coombes: Two races of Bean Goose *Anser arvensis* in Western Europe . . . 185
Robert Cushman Murphy: The Populations of the Wedge-Tailed Shearwater (*Puffinus pacificus*) . . . 189
Christian Jouanin: Remarques sur les Cormorans de la région australe américaine . . . 193
Jean Dorst: Considérations sur la systématique des Turdinés . . . 199
Theresa Clay: The Mallophaga as an Aid to the Classification of Birds with Special Reference to the Structure of Feathers . . . 207

## Migration and Orientation

Rudolf Drost: Study of Bird Migration 1938—1950 . . . 216
A. Landsborough Thomson: Reproduction, Migration and Moult: Factors Controlling the Annual Cycle in Birds . . . 241
R. E. Moreau: The Migration System in Perspective . . . 245
Ernst Schüz: Überblick über die Orientierungsversuche der Vogelwarte Rossitten (jetzt: Vogelwarte Radolfzell) . . . 249
Gustav Kramer: Eine neue Methode zur Erforschung der Zugorientierung und die bisher damit erzielten Ergebnisse . . . 269
Gustaf Rudebeck: Some notable factors concerning the migration of palaearctic birds . . . 281
Axel M. Hemmingsen: The Relation of Spring Migration to Day Length and Solar Radiation . . . 284
Axel M. Hemmingsen: The Relation of Bird Migration in North Eastern China to Body Weight and its Bearing on Bergmann's Rule . . . 289
Carl Edelstam: The Ottenby Bird Station . . . 295
Richard Hylbom: Migration Period of Some Passerines Revealed by Daily Ringing Figures at Ottenby . . . 310
Gustaf Rudebeck: The migration of birds of prey in southern Sweden, particularly at Falsterbo . . . 317
R. B. Sibson: Some Aspects of Bird Migration in New Zealand . . . 320
Alfred Van Beneden: Quelques aspects de la Migration d'Août en Belgique 326
Torsten Malmberg: Bird Migration in NW Scania . . . 330
Gunnar Svärdson: Swift (*Apus apus* L.) Movements in Summer . . . 335
John Berry: Migration to North Norway of Barnacle Geese which had been bred in Scotland . . . 339
G. Bouet: Les Cigognes blanches de l'Afrique du Nord et leurs Migrations . . 341
Poul Jespersen: Contribution à la Connaissance de la Migration des Cigognes Blanches (*Ciconia ciconia* (L.)) en Afrique du Nord . . . 344

Axel M. Hemmingsen: Observations on the Migration of the Eastern White Stork (*Ciconia ciconia boyciana* Swinhoe) . . . . . . . . . . . . . . . 351

Round Table Conference on Bird Ringing . . . . . . . . . . . . . . . 354
Bird-Ringing Schemes compiled by W. Rydzewski . . . . . . . . . . 356

## Behaviour

N. Tinbergen: Recent Advances in the Study of Bird Behaviour . . . . . . 360
Eric Fabricius: Some Experiments on Imprinting Phenomena in Ducks . . . 375
Holger Poulsen: Inheritance and Learning in the Song of the Chaffinch, *Fringilla coelebs* L. . . . . . . . . . . . . . . . . . . . . . . 380
O. Koehler: Vögel erlernen unbenannte Anzahlen . . . . . . . . . . . . 383
Dieter Burckhardt and Joseph A. Murnin: The Display of the Satin Bowerbird, *Ptilonorhynchus violaceus* Vieill. . . . . . . . . . . . . . . . . . 393
Holger Poulsen: Colourfilms: The Greeting Ceremony of the Shoe-Billed Heron, *Balaeniceps rex* L. Gd. and the Courtship Display of the Condor, *Vultur gryphus* L. . . . . . . . . . . . . . . . . . . . . . . . . 396
Fritz Steiniger: Tierpsychologische Beobachtungen bei der Photographie freilebender Vögel . . . . . . . . . . . . . . . . . . . . . . . . . . 398

## Ecology

David Lack: Population Ecology in Birds. A Review . . . . . . . . . . . 409
James Fisher: The changes in the distribution of the fulmar (*Fulmarus glacialis*) 449
James Fisher and H. G. Vevers: The Present Population of the North Atlantic Gannet (*Sula bassana*) . . . . . . . . . . . . . . . . . . . . . . . 463
A. Keve and M. D. F. v. Udvardy: Increase and Decrease of the Breeding Range of Some Birds in Hungary . . . . . . . . . . . . . . . . . . . . . . 468
J. Peitzmeier: Beobachtungen über Klimaveränderungen und Bestandsveränderungen einiger Vogelarten in Nordwestdeutschland . . . . . . . . 477
Einari Merikallio: Der Einfluss der letzten Wärmeperiode (1930—49) auf die Vogelfauna Nordfinnlands . . . . . . . . . . . . . . . . . . . . . . 484
Pekka Grenquist: On the Recent Fluctuations in Numbers of Waterfowl in the Finnish Archipelago . . . . . . . . . . . . . . . . . . . . . . . . 494
Gunnar Svärdson and Sigfrid Durango: Spring Weather and Population Fluctuations . . . . . . . . . . . . . . . . . . . . . . . . . . . . 497
Finnur Gudmundsson: The Effects of the Recent Climatic Changes on the Bird Life of Iceland . . . . . . . . . . . . . . . . . . . . . . . . . 502
Finn Salomonsen: The Immigration and Breeding of the Fieldfare (*Turdus pilaris* L.) in Greenland . . . . . . . . . . . . . . . . . . . . . . . 515

Ilmari Välikangas: The Expansion of the Greenish Warbler (*Phylloscopus trochiloides viridanus* Blyth) in the Baltic Area, especially in Finland, towards North and Northwest, and its Causes . . . . . . . . . . . . . . . . 527

Alfred O. Gross: The Herring Gull - Cormorant Control Project . . . . . . 532

Josselyn Van Tyne: The Distribution of the Kirtland Warbler (*Dendroica kirtlandii*) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 537

Per Olof Swanberg: Food Storage, Territory and Song in the Thick-billed Nutcracker . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 545

H. R. Tutt: Data on the Excavation of the Nest Hole and Feeding of the Young of Green Woodpecker (*Picus viridis*) . . . . . . . . . . . . . . . . . . 555

Violet Maxse: The British Long Tailed Tit (*Ægithalos caudatus roseus*). How its Nest is Built . . . . . . . . . . . . . . . . . . . . . . . . . . 563

E. J. L. Hallstrom: The black Cockatoo . . . . . . . . . . . . . . . . 567

H. Noll: Der Rhytmus in den Brutzeiten einiger schweizerischer Vögel . . . 571

A. Schifferli: Vom Brutvogelbestand eines Hochgebirgswaldes im Wallis . . 574

D. E. Sergeant: Ecological Relationships of the Guillemots *Uria aalge* and *Uria lomvia* . . . . . . . . . . . . . . . . . . . . . . . . . . . . 578

R. Spärck: The Food of the North-European Gulls . . . . . . . . . . . . 588

E. van Koersveld: Difficulties in stomach analysis . . . . . . . . . . . 592

M. D. F. v. Udvardy: Heat Resistance in Birds . . . . . . . . . . . . . 595

## Regional Faunas

E. M. Nicholson: Birds of the North Atlantic . . . . . . . . . . . . . 600

Bernt Løppenthin: Sea Birds of the Persian Gulf . . . . . . . . . . . 603

Peter Scott: Geese in the Canadian Arctic . . . . . . . . . . . . . . . 611

Arthur A. Allen: The Curlew's Secret . . . . . . . . . . . . . . . . . . 613

Holger Holgersen: On the Birds of Peter I. Island . . . . . . . . . . . 614

Yngvar Hagen: Birds of Tristan da Cunha . . . . . . . . . . . . . . . . 617

## Miscellaneous

Arthur A. Allen: Progress in Bird Photography and Sound Recording . . . 625

Robert Cushman Murphy: The Moa Deposits of Pyramid Valley Swamp, New Zealand . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 628

Adolf Kleinschmidt: Über eine Rekonstruktion des Schädels von *Archaeornis siemensi* Dames 1884 im Naturhist. Museum, Braunschweig . . . . 631

Ernst Sutter: Growth and Differentiation of the Brain in Nidifugous and Nidicolous Birds . . . . . . . . . . . . . . . . . . . . . . . . . . . 636

K. G. Wingstrand: The Structures in the Avian Pituitary Responsible for the Transfer of Impulses from the Nervous to the Hormonal System . . . . 645
Adolf Kleinschmidt: Das Flugvermögen der seglerartigen Vögel (*Macropterygidae*) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 647
Peter Scott: Researches of the Severn Wildfowl Trust . . . . . . . . . . 648
Grace E. Barstow Murphy: Conservation on Ornithological Programs . . . 652
Rudolf Kuhk: Zur Mitarbeit nichtfachlicher Kräfte in der Ornithologie . . . 656

The Permanent Executive Committee 1950—1954 . . . . . . . . . . . . . 659
The International Ornithological Committee . . . . . . . . . . . . . . . . 659
Règlement des Congrès Ornithologiques Internationaux . . . . . . . . . . 661

Members of the Xth International Ornithological Congress in front of the University Building at Uppsala.

# The Xth International Ornithological Congress

## The Congress at Uppsala 10th–17th June 1950

International ornithological congresses have been held in Vienna 1884, Budapest 1891, Paris 1900, London 1905, Berlin 1910, Copenhagen 1926, Amsterdam 1930, Oxford 1934 and Rouen 1938. At the IXth Congress at Rouen it was decided that the next congress should be held in USA and Dr. Alexander Wetmore, Washington, was appointed as its President. As it was thought after the second world war that a congress in USA would not be attended by any great number of ornithologists from outside America because of the economic conditions and the difficulties in obtaining currency in post-war Europe, the Swedish Ornithological Association (Sveriges Ornitologiska Förening) was called upon to organize the Xth Congress. Since the Swedish Government had promised financial support, the Association decided at its annual meeting on 5th March 1949 to undertake the task. At the suggestion of the Association the Permanent Executive Committee appointed the President of the Association, Professor Sven Hörstadius, Uppsala, as the Secretary General of the Congress.

The Association appointed the following Organizing Committee: Professor S. Hörstadius, Uppsala, Chairman; Count N. Gyldenstolpe, Stockholm, Vice Chairman; S. Forselius, Uppsala, Secretary; K. Curry-Lindahl, Stockholm (Editor of "Sveriges Natur"); E. Wide, Stockholm, Treasurer; S. Durango, Täby; Professor S. Ekman, Uppsala; B. Haglund, Stockholm (Editor of "Svensk Jakt"); G. Otterlind, Fiskebäckskil (Editor of "Vår Fågelvärld"); G. Rudebeck, Lund; P. O. Swanberg, Skara; Dr. G. Svärdson, Stockholm. Mr. Sten Forselius was chosen as Assistant Secretary General for the Congress. Mrs. Marie-Louise Lundberg was employed as Manageress of the Congress Bureau.

It was decided, that the Congress should be held at Uppsala. There were several reasons for this decision. In a larger city, such as Stockholm, the members of the Congress would be more scattered and would not have as much opportunity of being together as in a smaller town. Bearing in mind that the greater part of the members would probably receive very limited currency allowances, it was also desirable to arrange their stay as cheaply as possible. At Uppsala meals could be obtained at a lower price than in Stockholm. Admittedly the supply of hotel rooms was extremely limited at Uppsala, but on the other hand cheap rooms could be obtained in students' lodges, which advantage was considered greater than the disadvantage that those members with more exacting requirements would have to be content with modest quarters. Regarding the date of the Congress, it could not commence until about 10th June, as the students' lodgings would not be free earlier. On the other hand the week 10th–17th June would be rather late in the season with regard to the number of birds that would be observed during the excursions after the Congress.

Between July and September 1949 about 6 500 invitation programs were distributed. They were sent to a great number of ornithologists, to the National Museum of Natural History in every country, to ornithological associations, etc. In some countries the program was included as a supplement in an issue of an ornithological magazine. In many countries an ornithologist undertook to forward the program to persons interested. Ornithological and other natural history magazines were requested to insert an item about the Congress with particulars as to the address for obtaining further information. It was stated in the program that preliminary registration should be made by 28th February at the latest and the Congress fee, Sw. cr. 25, should be paid in by 15th April at the latest. In addition particulars were given about prices for meals, different kinds of rooms, fares, etc., as well as the excursions, which would be arranged before, during and after the Congress.

Immediatly preceding the Congress, on 8th and 9th June, the International Committee for Bird Preservation (Comité International pour la Protection des Oiseaux) held its first meeting after the second world war. (The European Section had met in 1947 in London and 1948 in Paris.) The Chairman at the meeting was Mr. J. Delacour, New York, and the Secretary Miss Phyllis Barclay-Smith, London. The meeting was attended by about seventy persons from 17 countries. Most of those attending were also members of the Congress. On Saturday June 10th the City Council of Uppsala gave a dinner for all the members of the Committee at Östgöta Nation.

About 410 preliminary registrations were received for the Congress, but only 377 of these were confirmed; 25 of that number later were prevented from coming, in addition to which 15 took part only in the excursions. The number attending at Uppsala therefore amounted to 337. 27 countries were represented with the following figures: Argentina 1, Australia 2, Austria 3, Belgium 10, Canada 4, Denmark 32, Dutch Guiana 1, Egypt 1, Finland 9, France 20, Germany 30, Great Britain 73, Greece 1, Hungary 1, Iceland 1, India 1, Ireland 7, Italy 2, Liechtenstein 1, The Netherlands 33, New Zealand 2, Norway 4, Spain 1, Sweden 83, Switzerland 15, USA 35, Venezuela 4. Among those who were prevented from coming were all the persons who had made applications from Poland, Czechoslovakia, Hungary and Yugoslavia.

As all the matters concerning the international congresses are decided by the International Ornithological Committee and its Permanent Executive Committee, it was first decided not to issue invitations for the sending of delegates. Requests for invitations were received, however, from many institutions and societies, as members with the support of such an invitation would find it easier to obtain travel grants and currency allowances, so invitations were issued to those societies which had requested them, as well as to other purely ornithological societies and to natural history museums. In addition a great number of delegates gave notification of their intention to attend the Congress. A list of the delegates present is given on page 42.

At the joint meetings for the whole Congress on the 10th, 12th, 13th and 17th June, the "Röda Kvarn" Cinema was used as a Congress Hall. On the 15th and 16th the work was divided into two sections as well as a Round Table Conference on Bird Ringing, all of which were held in the lecture halls in the main building of the University. The 11th and 14th were devoted entirely to excursions. The Congress Bureau, which also included a bank and a post office, was housed in a students' corporation building, Värmlands Nation, situated near the Cathedral between the Congress Hall and the University. In this building there were commodious club rooms at the disposal of the members and here, too, was one of the Congress Dining Halls, while the other was in the next house.

The Congress was opened by the President, Dr. A. Wetmore, on Saturday the 10th of June at 3 p. m., after which the Secretary General in the capacity of President of the Swedish Ornithological Association welcomed those present to Sweden and Uppsala. Some telegraphic greetings were then presented. Dr. Wetmore's Presidential Address dealt with "Recent additions to our knowledge of prehistoric birds" (p. 51), following which Professor Hörstadius gave an "Introduction to Swedish ornithology" (p. 75). After that P. O. Swanberg spoke on "Food storage, territory and song in the Thickbilled Nutcracker" (p. 545). The opening session was concluded by a "Colour film on Swedish wild life" by Bertil Haglund.

The Organizing Committee had invited four scientists, who are eminent specialists in their branches, Dr. E. Mayr, Prof. R. Drost, Prof. N. Tinbergen and Dr. D. Lack, to give lectures on bird speciation, migration, behaviour, and ecology respectively. The other papers of which notification had been received were divided into groups: Evolution and systematics, Bird migration and orientation, Bird behaviour, Population dynamics, Ecology of certain species, Regional faunas, Palaeontology, anatomy, physiology and various topics.

The proceedings began on Monday the 12th of June with Dr. Mayr's lecture on "Speciation in birds" (p. 91), in Dr. Mayr's absence read by Dr. R. C. Murphy, followed by four papers from the group dealing with Evolution and systematics. The afternoon was devoted to Migration and orientation with Prof. Drost's lecture (p. 216) as the opening address. On Tuesday morning Prof. Tinbergen presented his report on "Recent advances in the study of bird behaviour" (p. 360), and after lunch Dr. Lack spoke on "Population ecology" (p. 409). With regard to the other papers, reference should be made to the program p. 34–41, from which it will be observed that the proceedings on Thursday and Friday were divided into two sections.

The Organizing Committee is extremely grateful to Messrs. Mayr, Drost, Tinbergen and Lack for their kindness in undertaking the task of giving the Congress surveys of the present position of science in the domains in question. As a result the proceedings of the Congress were greatly enhanced by their lectures, which have been published here unabridged and with detailed lists of references.

It might seem that the number of addresses and reports was far too big for a one week congress. The greater part, however, were short papers lasting 10–15 minutes, and as the lecturers were urged not to exceed their time as well as being warned by signals from a red lamp before and at the close of the stated time, the sessions were not unreasonably long and tiring. The contributions to the debate are described in the Proceedings by each respective speaker, who prepared an account himself of his contribution immediately after the conclusion of the debate.

In the evenings of the 12th, 13th and 15th a great number of extremely beautiful and interesting films in black and white and in colour were shown at the University (see program p. 34), and were received with much applause. Dr. I. Homoki Nagy's remarkably fine colour pictures of Hungarian birds were also shown, to the very great delight of the audience.

In the Entrance Hall of the University during the congress week an exhibition was held of Swedish bird photographs, arranged by Mr. K. Curry-Lindahl, and in the University Library the Librarian of the Swedish Ornithological Association, Mr. S. Armington, had arranged with the assistance of the library officials an exhibition of Swedish ornithological literature from Linné to present times. A number of Olof Rudbeck the Younger's famous bird plates were also shown (see p. 76). The members of the

Congress had free admission during the week to the museum of the Zoological Institution, to the Biological Museum of the city with its display of Swedish fauna in natural surroundings, as well as to Linné's house and garden at Svartbäcksgatan. A wreath was laid on Linné's tombstone in the floor of the Cathedral.

On Friday the 16th of June a Round Table Conference on Bird Ringing was held, see p. 354.

On the same day, as a result of Dr. Salomonsen's paper on a Nomenclature Controversy, the Chairman suggested that any Congress Members interested in the subject should meet that afternoon to decide what action might be taken to attain stability in nomenclature. At the subsequent meeting, with Dr. de Beaufort in the chair, it was clear that there was an overwhelming majority in favour of attaining stability by referring contentious cases to the International Commission on Zoological Nomenclature. An Ad Hoc Committee of four was formed to collect and submit to the International Commission those cases in avian nomenclature which were causing confusion through lack of stability. The Committee elected comprised: Col. Meinertzhagen, Chairman, Dr. Stresemann, Dr. Berlioz and Dr. J. Zimmer.

During the congress week the International Ornithological Committee and the Permanent Executive Committee each held two meetings. The Chairman and Secretary for the different sessions are shown in the program, p. 34. Owing to death or other causes the following persons have left the International Ornithological Committee, which comprises 100 members: Argentina: R. Dabbene. Canada: J. Fleming, P. Taverner. Estonia: M. Harms. Germany: C. Hellmayr, O. Heinroth, F. von Lucanus, O. Neumann, H. Reichling. Great Britain: E. Stuart Baker, A. Evans, F. Jourdain, P. Lowe, W. Sclater, A. Sladen, C. Ticehurst, H. Witherby. Hungary: F. Csorgey, J. Schenk. Malaya: F. Chasen. Netherlands: N. Tinbergen. Norway: H. Schaanning. Poland: K. Wodzicki. South Africa: M. Bigalke, A. Roberts. Sweden: H. Granvik, E. Lönnberg. Switzerland: O. Meylan. Czechoslovakia: Count Seilern. USA: F. Chapman, J. Grinnell, H. Oberholser, J. Phillips, A. van Rossem, L. Stejneger. The previous representative for East Africa, R. E. Moreau, was transferred to Great Britain, K. Lorenz and M. Sassi were transferred from the German group to Austria, and J. Delacour, who was formerly French, now became a representative for USA. Newly elected members were: Brasil: O. Pinto. Canada: H. Lloyd, L. L. Snyder. Chile: R. A. Philippi B. Colombia: A. Dugand. Denmark: K. Paludan. Finland: P. Palmgren. France: R. D. Etchécopar. Germany: G. Kramer, O. Koehler. Great Britain: P. Barclay-Smith, J. Huxley, D. Lack, A. Landsborough Thomson, W. H. Thorpe, V. C. Wynne-Edwards. Hungary: A. Keve. Iceland: F. Gudmundsson. India: Sálim Ali. Kenya: J. G. Williams. Malaya: C. A. Gibson-Hill. Netherlands: C. Junge, K. H. Voous. New Zealand: R. A. Falla. Norway: H. Holgersen. South Africa: J. Vincent. Spain: F. Bernis M. Sweden: S. Bergman, G. Rudebeck, G. Svärdson. Switzerland: P. Géroudet, A. Portmann, A. Schifferli. USA: H. Deignan, A. H. Miller, A. L. Rand, J. Van Tyne. Venezuela: W. H. Phelps. The complete list of the members of the Committee at the end of the Congress is to be found on p. 659.

The Permanent Executive Committee of the International Committee was appointed and consists of the President and Secretary General elected for the next congress as well as six members (see statutes p. 661). As Dr. Wetmore was chosen as a member, Dr. R. C. Murphy resigned membership in order to avoid, in accordance with the statutes, the election of two Americans. Whereupon the former members A. Ghigi, Italy, R. Meinertzhagen, Great Britain, and E. Stresemann, Germany, were reelected. J. Berlioz, France, was chosen as successor to the late E. Lönnberg, Sweden. The Secretary General of the Congress at Rouen, J. Delacour, USA, was re-elected to occupy the sixth vacancy.

It was decided that the next congress should be held in 1954. Invitations had been received from India, Italy and Switzerland. The Committe gratefully accepted the Swiss offer to arrange the XIth Congress. Dr. A. Landsborough Thomson, London, was elected as its President.

Sunday the 11th of June was devoted to a whole day excursion to the archipelago off the town of Norrtälje. 290 members left Uppsala by bus at 8 a.m. and after a 1 $^1/_2$ hour ride went on board S/S "Norrskär," which sailed via the long and narrow Norrtälje Bay first to the inner archipelago with its large islands and then to the outer archipelago with the hundreds of small islands and holms. It was a day of brilliant sunshine and blue skies, so that the archipelago was at its very best. With its countless islands great and small, often rocky, nearer the coast covered with pine trees, further out with hardwood trees, this constitutes an unusual type of habitat, which was undoubtedly something new for most of the foreign guests. The day was a disappointment, however, from an ornithological point of view on account of the extremely high and cold wind, which made the greater number of the birds, that can usually be observed from the boat, remain hidden. A stay was made for a couple of hours on the island of Idö, where a considerable number of birds were observed during walks in the shore meadows and the woods. See table on p. 28 for birds observed during the day. On the return journey busses met the boat at Räfsnäs, and Uppsala was reached about 5 p.m.

On Wednesday the 14th of June the members were invited to go on a bus excursion to a coniferous forest region north of Uppsala. As there is but little result when such an excursion is made in the middle of the day, a large group of about 160 persons left at midnight on Tuesday evening. The expedition was planned to visit the neighbourhood of the famous iron mines at Dannemora, about 50 km (30 miles) north of Uppsala, where the members were divided into a number of groups each with its own guide. Here there was an opportunity of studying bird life in cultivated land and the adjoining hardwood belt, but above all the wild life in large coniferous forests, where several groups had the privilege of seeing not only a great number of species of birds (see table p. 28) but also elk and roe deer. Some small lakes were visited in the forest and on the return journey, after breakfast at Dannemora Hotel, Lake Vissjön with its wide-stretching marshes. 100 persons, for whom there had not been room in the first party, started at 2 p.m. on Wednesday. Lake Vissjön was then visited first, after which dinner was served at Dannemora Hotel and the walk through the forests took place during the late hours of the evening, when the birds are once more active in the long twilight. In spite of the great number of persons, who took part in this excursion, the results can be said to have been satisfactory owing to the division into smaller groups. The long twilight and the light night were probably a unique experience for most of the members, who had not previously seen a summer night in such a northern latitude.

The Congress ladies on Thursday the 15th were the guests of the Congress on a trip to Skokloster, a famous castle. The journey was made by motorboat, first on the lower reaches of the River Fyrisån and then through the bights and channels of Lake Mälar to Skokloster. This castle was built by one of the military commanders of the Thirty Years' War, Field Marshal Carl Gustaf Wrangel, and is remarkable because the entire building with all its furniture and valuable collections has been practically unchanged since the 17th century. After the visit to the castle, lunch was served before the return journey was commenced.

On Friday afternoon the members of the Congress were invited to go on an excursion by bus to Gamla Uppsala, the cult-centre of Sweden in heathen times, famous for its mighty grave mounds from the 6th century B.C., the Kings' Mounds. Tea was served at Gamla Uppsala. After tea Linné's charming summer home Hammarby was visited, which with its lovely red timber buildings, its garden park and little museum, built by Linné of stone on the hill behind the farm on account of the danger of fire, will undoubtedly be a cherished remembrance for all the ornithologists who visited it.

At 8 p.m. on Friday the members assembled for the Congress Dinner in the hall of the Vasa Castle. His Excellency The Governor of the Province of Uppsala, Mr. H. Kjellman, presided at the dinner, which was given by the Swedish Ornithological Association. In his speech of welcome in French and English the Governor spoke amongst other things of the history of the hall, how the coronation banquets were held there in the old days after the coronation in the Cathedral, and how Queen Christina gave up her crown in the selfsame hall in 1654 before she departed for Rome. After a speech by the Secretary General, in the capacity of President of the Swedish Ornithological Association, the President of the Congress, Dr. Wetmore, expressed the gratitude of those present to the Secretary General, the Assistant Secretary General, the staff of the Bureau, the guides on the excursions, the organizers of the exhibitions and others for the work they had done on behalf of the Congress. Towards the end of the dinner "Allmänna Sången", that is to say the undergraduates' choir, marched in in their white caps and sang some quartets. Men and women undergraduates from "Philochoros" in colourful peasant costumes gave a display of Swedish folk dances after the conclusion of the repast.

The concluding session on Saturday morning offered a varied program; see p. 41. After the last paper the President announced which persons had been chosen as Committee Members by the International Ornithological Committee to succeed retiring members (see p. 17), and which persons had been elected as Members of the Permanent Executive Committee (p. 18). Professor S. Hörstadius was elected as Additional Member of the latter. Finally the decision of the International Ornithological Committee to hold the next congress in 1954 was announced, and that the offer from Switzerland to arrange the Congress had been accepted. It was stated that Dr. A. Landsborough Thomson had been elected as the President of the Congress. Professor A. Portmann, Basel, was chosen as its Secretary General.

Following this Dr. Wetmore declared the Xth International Ornithological Congress to be concluded.

A great number of the members left the same evening or the next morning for the excursions in different parts of the country.

## Excursions before and after the Congress

Before the Congress trips were arranged for two days from the university town of Lund in Skåne, and also excursions to either the islands of Öland or Gotland in the Baltic. Immediately after the conclusion of the Congress a further excursion was made to Öland and one to Gotland, as well as an excursion in the provinces of Närke and Värmland, two consecutive excursions with headquarters at Handöl in the province of Jämtland, one to Ammarnäs in Mid-Lappland, two consecutive excursions in the neighbourhood of the famous mining town of Kiruna, and two consecutive ones with accommodation at Abisko Turiststation in Northern Lappland. The location of the areas may be seen from the map p. 28. On this map each excursion, including the two previously mentioned from Uppsala during the Congress, has been provided with a number in Roman figures. The birds which were observed during the excursions are listed in the table on p. 29–33, in which the numbers of the columns correspond to the numbers on the map on p. 28. In the following short account of the excursions, the birds are not dealt with so that reference should be made to the respective column in the above-mentioned table. This table can, perhaps, be useful to persons who wish to visit Sweden in the future for studying birds, as it may give a certain idea of the composition of the bird fauna in some different parts of the country.

The Swedish Ornithological Association had published under the editorship of Sven Armington a list of Swedish birds, including the scientific, English, French, German and Swedish names: Nomina Avium Sveciae (Bokförlaget Svensk Natur, Stockholm 1950, price Sw. crowns 1.50) to assist the persons taking part in the excursions, who represented many countries and languages. This list was given to all the members of the Congress.

### *Excursions from Lund in the province of Skåne (Scania), 8th–9th June*

The persons taking part in these excursions were: Miss C. Acland, A. Allen, Mrs. A. Allen, P. Armitage, Miss E. Baxter, J. De Maerschalk, M. Dijkstra, F. Edmond-Blanc, A. Bryson, H. Course, G. de Greef, J. Ferdinand, C. Ferry, Mrs. C. Ferry, A. Gross, Mrs. A. Gross, S. Haftorn, Y. Hagen, L. Hoffman, Collingwood Ingram, Mrs. J. Kelly, Miss S. Knecht, J. Lepiksaar, Mrs. J. Lepiksaar, W. Logan-Home, Mrs. W. Logan-Home, Miss V. Maxse, R. E. Moreau, Mrs. R. E. Moreau, A. Parsons, H. Payton, T. Pearse, Mrs. T. Pearse, Miss K. Price, C. Rawcliffe, J. Stanford, Mrs. J. Stanford, J. Taapken, N. Tinbergen, C. Wells, Mrs. C. Wells, A. Wetmore, H. von Vietinghoff-Riesch, A. B. Wigman, W. Vogt, Mrs. W. Vogt.

On the morning of the 8th of June the members met at the Zoological Institute at Lund, where Professor Bertil Hanström made a speech of welcome and Dr. Gustaf Rudebeck gave a short introduction to the bird fauna of Skåne. The busses left at 9 a.m. in perfect summer weather eastwards via Dalby for Stensoffa Gård, where the members walked through hardwood forests and damp meadowland down to the marshy jungles and clear waters of Lake Krankesjön. About 11 o'clock they continued to Åmansbro on the northern side of Lake Sövdesjön, where a short stop was made on the moorlands beside the lake. After lunch at Snogeholm Castle the busses drove back northwards to Karup meadows in the valley of the Klingvallsån River, and here there were several hours' walk over the sandy grounds and wet meadows, that are so rich in birds. The return journey was made via Malmö, where Curator Helge Bergman showed the magnificent collections of birds in the Malmö Museum to the members and the Museum Board invited them to tea in the Riddarsalen at Malmöhus. The guides were Gustaf Rudebeck and Torsten Malmberg.

On the 9th of June the members had a choice between two excursions. One was of a purely ornithological nature. The journey was made by bus southwards first to the beech forest area round Lake Fjällfotasjön and then direct to Falsterbo, where the members walked across the sandy headland to the most southwesterly point in Sweden, Ulanabben. After lunch at Skanörs Gästgivaregård a visit was also paid to Flommen, the marshy fields inside the sand dunes to the west of the town. The guides were Gustaf Rudebeck and Torsten Malmberg.

The other excursion was intended for members of the Congress who were interested in historical buildings. It included visits to a number of castles and churches in Skåne. The buses drove from Lund to Skarhult Castle and from there via Gårdstånga Church to Övedskloster Castle and then to Östarp, where lunch was served. After lunch the excursion was continued to the churches at Everlöv and Dalby and then via Torup Castle back to Lund. The guide was Torsten Herner.

### *Excursions on Öland, 3rd–7th and 18th–22nd June*

Persons taking part 3rd–7th June: E. Cohen, H. Giersberg, P. Grenquist, F. Gudmundsson, Miss R. Gustafson, A. Hemmingsen, L. Hoffman, Miss V. Maxse, J. Mills, Mrs. J. Mills, T. Pearse, Mrs. T. Pearse, R. Serlachius, J. Steinbacher, F. Steiniger, C. Wells, Mrs C. Wells, I. A. Williams, Mrs I. A. Williams.

18th–22nd June: Miss P. Barclay-Smith, Miss E. Baxter, A. Bryson, H. Course, R. Drost, J. Espana Cantos, J. A. Eygenraam, R. Heath, Miss C. James, R. Kuhk, W. Logan-Home, Mrs. W. Logan-Home, H. Payton, C. Rawcliff, E. Schüz, R. Sibson, Mrs. R. Sibson.

The guide was Claes Ramel. A preparatory exploration of the terrain had been made not only by the guide but also by Carl Edelstam, who was, however, prevented by an injury, sustained while reconnoitring, from taking part both in the excursions and the Congress.

The members were provided with accommodations at Vickleby on the west coast, 35 km south of Borgholm, and situated on the edge of the so called Alvaret, the largest steppe of a uniform character of northern Europe, which from a zoological as well as botanical point of view exhibits several unique features, especially in the way of relics. One day was devoted to Alvaret. Thanks to the kindness of two Swedish botanists, Dr. Degelius and Mr. Ståhle, the participants were informed of the botanical characteristics of this steppe during the tours over Alvaret. The bird fauna is poor both in species and individuals. A strong concentration of the bird fauna of this steppe area is found at the numerous swamps. During one of the days a tour was made by bus to the northern part of Öland, where swamps of a different type were studied. The same day the bay of Södviken on the east coast was also visited. One day was devoted to the deciduous forest at Ottenby, as well as to the Ottenby Bird Station at the southern point of Öland. Finally a tour was made to the old harbour of Beijershamn. The mixture of sea-birds and fresh-water-birds breeding here is the most noticeable feature of this place.

### *Excursions on Gotland, 3rd–7th and 19th–23rd June*

Participants 3rd–7th June: E. Chalif, Mrs. E. Chalif, H. Davis, J. Fisher, H. Hellebrekers, W. Hellebrekers, P. Jespersen, Mrs. P. Jespersen, E. v. Koersveld, P. Olufsen, Mrs. P. Olufsen, S. Persson, R. T. Peterson, Mrs. R. T. Peterson, B. Runnerström, M. Schulz, M. J. Tekke, M. Tiedemann, Mrs. M. Tiedemann, C. Tillisch, H. Tutt, J. Van Tyne, Mrs. E. Welti, Miss A. Wild.

19th–23rd June: R. van der Burg, Mrs. J. A. Fischer, Miss E. Forster, A. O. Gross, Mrs. A. O. Gross, Lord Hurcomb, J. Jacobs, Mrs. J. Kelly, R. E. Moreau, Mrs. R. E. Moreau, T. Pearse, Mrs. T. Pearse, R. Pough, Mrs. R. Pough, G. v. Rokitansky, L. Sargent, Mrs. L. Sargent, M. Sassi, W. Snow, J. Stoffel, G. Thibout, Mrs. G. Thibout, Miss G. Thibout, Mrs. P. Thibout, C. Tucker, Mrs. C. Tucker.

The guides were Gösta Håkansson and B. O. Jansson, Visby. The participants stayed at Visby, whose town wall, ruins and other sights were visited with a cicerone, in addition to which many birds were observed in the immediate surroundings of the town. The first evening a bus tour was made to a high point commanding a fine view, Högklint, above the cliffs south of Visby. Here Dr. Bengt Pettersson described the geological features for the members of the second excursion. On the second day a visit was paid to Stora Karlsö Island which has the only bird cliff in Sweden and has besides a great quantity of birds, which were observed under the guidance of Josef Nordström, the keeper of the island. The next day there was a bus trip to the leafy meadows at Alvena, Vallstena Parish, as well as to Lina marsh. After lunch at Ljugarn the journey continued to Lausviken on the east coast, famous for its large flocks of *Branta leucopsis*, which rest there every year but which had already disappeared. The fourth day was devoted to a visit to Martebo marsh where many species of aquatic birds breed. Accommodation for the night was provided on Fårö Island. On the last day a walk was taken among the sand dunes of Ullahau before lunch and in the afternoon Långhammars was visited.

### *Excursion in Närke and Värmland, 18th–24th June*

Persons taking part: Sálim Ali, D. Burckhardt, T. D. Mills, G. Parsons, A. Van Beneden.

The members arrived at Örebro in Närke on the morning of the 18th by train. After lunch the Örebro City Bird Sanctuary at Oset was visited. The morning of the following day was devoted to forest, river and lake biotopes, amongst other places the bird lake Tysslingen. The journey then continued to Hasselfors, where AB Hasselfors Bruk had invited the members to dinner, after which Gåsjömossen was visited amongst other places. The next morning a visit was paid to Hasselfors sawmills before continuing to Stormossen in Visnums-Kil and Kilsviken of Lake Vänern.

The guide for the Närke section of the excursion, Erik Rosenberg, left the group at 5 p.m. at Kristinehamn in the hands of the new guides Dag Hannerz, Rolf Hannerz and Bo Österlöf.

The party continued by car to Uddeholm, where the Uddeholm Company had invited the members to dinner, and then via Föskefors Manor in Ekshärad to their quarters for the night at Bergsäter. On the 21st of June a morning excursion was made to the plains and swamps at Hamratjärn and the park region round Föskefors as well as to other forest and marsh areas. Next day there was an excursion over Bäckelberget (460 m above sea level) and then to the forest village at Granberget, from which place a ten kilometre walk was taken across country across the boundary of the province into Dalarna, return journey by car. On the last day the group returned to Uddeholm and a visit was paid to two eyries of *Falco peregrinus*, both of which, however, unfortunately had been destroyed.

During this excursion great hospitality was accorded to the participants as regards meals, accommodation and motor trips by ornithologists at Örebro, by Hasselfors Bruk, the Uddeholm Company and its officials, as well as many private persons.

### *Excursions to Handöl, Jämtland, 19th–24th and 25th–30th June*

Participants 19th–24th June: G. Brouwer, Mrs. G. Brouwer, E. Cohen, R. De Laveley, H. Dirkx, W. van Dobben, Miss J. M. Ferrier, F. Gudmundsson, Miss I. Jansson, E. Jonsson, Miss S. Knecht, Miss C. Longfield, T. Malmberg, Mrs. T. Malmberg, Miss V. Maxse, B. Runnerström, P. Scott, Miss P. Talbot-Ponsonby, A. Landsborough Thomson, Mrs. A. L. Thomson, Miss U.-B. Thulin, C. Tillisch, E. Tobiesen, Mrs. E. Tobiesen.

25th–30th June: Miss G. Höij, Miss I. Jansson, Mrs. E. Lundh, Miss V. Maxse, J. Stanford, Miss U.-B. Thulin.

The cicerones were Lars Faxén and Carl Persson, while Lars Melander acted as reconnoitrer and assistant guide.

Handöl is situated between Mt. Snasahögarna (1 463 m.) and Lake Ånn in the western part of Jämtland. More than half of Lake Ånn is extremely shallow as the rivers are bringing down great masses of sediment from sediment terraces formed during the melting period of the inland ice. The immediate surroundings of Lake Ånn lie in the coniferous forest region with spruce as the dominating coniferous tree but often richly mixed with birches, with a ground vegetation of heath or meadow type. Because of the flatness of the landscape in this region forests often give place to mires of great extent, fens as well as mosses. The upper limit of the coniferous forest lies about 650 m above sea level here. Then the subalpine birch forest region begins, reaching to about 800–850 m — cf. the tree line at Abisko further north, p. 28. Above the birch forest follows the low alpine region with heaths of *Empetrum* and *Myrtillus* and, on the slopes with a stronger flow of soligenous water, more hygrophilous communities. Above 1 100 m the low alpine region gives place to the middle alpine region with a more and more scattered vegetation and with naked shelves and blocks of rock. The summits of the mountains in the district of Lake Ånn do not reach the sterile high alpine region, as in the Abisko district. During the excursions the participants studied the zonation of the avifauna in the various regions and in the lakes.

### *Excursion to Ammarnäs, Lappland, 19th–24th June*

Participants: J. Cunningham, Mrs. J. Cunningham, S. Cunningham, L. Ferdinand, T. Feremans, C. Ferry, Mrs. C. Ferry, S. Flodmark, E. Hansen, T. Herner, T. Jacobsson, T. Lampio, Mrs. E. Lundh, Miss A. Mackie, H. Malcolmson, G. J. van Oordt, B. Palm, R. H. Reeh, F. Steiniger, O. B. Svane, E. Svennilsson, S. Thulin, L. Turtle, S. Ulfstrand, H. v. Vietinghoff-Riesch, H. Zetterberg.

The cicerone was Gustaf Rudebeck, reconnoitrers and assistant guides A. Enemar, G. Markgren, M. Markgren and E. Tarras-Wahlberg.

The village of Ammarnäs lies beside Gautsträsket, 400 m above sea level. Below the south east offset Stupipakte of Mt. Ammarfjäll, about ten km north west of Ammarnäs, lies Marsivagge, a spring-flooded tussocky swamp area with Salix vegetation along the Karsbäcken River, which flows through it and, after a steep course to the south, joins the River Tjulån, a tributary of the River Vindelälven, which forms a big delta beside Ammarnäs village. A few kilometres south of Ammarnäs lies treeless Mt. Ribovardo, approx. 1 000 m, with a steep precipice to the east. Rather more than ten km north east of Ammarnäs and 800 m above sea level lies the high valley of Råtakvagge, where the snow thaws late and the flora and fauna are of an arctic type. The higher coniferous forest follows the level valley of the Vindelälven River for about ten kilometres north from Ammarnäs, but for only a few kilometres along the Tjulån River and the Karsbäcken River, and climbs barely half way up the eastern side of Mt. Ribovardo. On the 19th of June the delta was visited and the Vindelälven River was followed for about 5 km to the north. The next day a walk was taken through the coniferous forest and to the top of Mt. Ribovardo. The 21st and 22nd of June were devoted to River Tjulån and Marsivagge. On the last day an excursion was made to the coniferous slopes west of the Vindelälven River as well as a walk to Råtakvagge.

### *Excursions to Kiruna, Lappland 18th–24th June and 24th–31st June*

Participants 18th–24th June: Mrs. M. Ehnberg, W. Hellebrekers, D. Lack, Mrs. D. Lack, L.-W. Masch, F. Salomonsen, A. Schifferli, D. Sergeant, M. v. Udvardy, Miss I. Werth.

24th–31st June: J. F. Barrington, E. Hansen, J. Harrison, A. Hemmingsen, B. Løppenthin, R. H. Reeh, C. Wells.

Guide: Björn Holm.

Immediately after their arrival at Kiruna the participants were taken by car to their quarters 16 km north east of the village of Paksuniemi, which in its turn lies on the Torneälven River south east of Jukkasjärvi church village. The quarters consisted of two road-labourers' cabins beside a little lake, not marked on the map. Military sleeping-bags had been provided. The cooking was done by the guide assisted by the other participants in the excursion. Trips were made from this camp in the great forests surrounding it and to swamps, to larger and smaller lakes, to a high ridge beside the Vittangiälven River as well as to low Mt. Rautusakara (639 m above sea level), which scarcely reaches above the tree line.

### *Excursion to Abisko, Lappland, 18th–25th June and 25th June–1st July*

Participants 18th–25th June: Miss C. Acland, Miss E. Adelholt, Miss P. Armitage, F. J. F. Barrington, J. Berry, F. Blatter, Mrs. B. Carnes, E. Chalif, Mrs. E. Chalif, C. de Worms, F. Edmond-Blanc, P. Engelbach, R. D. Etchécopar, J. Fisher, Miss Edith Godman, Miss Eva Godman, J. Harrison, H. Hellebrekers, A. Hemmingsen, L. Hoffman, F. Hüe, Collingwood Ingram, H. Johnson, Miss P. Klausen, E. v. Koersveld, G. Kramer, Mrs. G. Kramer, B. Løppenthin, C. M. Ogilvie, G. Olivier, Mrs. G. Olivier, O. H. Peall, Mrs. O. H. Peall, R. T. Peterson, Miss K. Price, J. K. Stanford, E. Stresemann, Mrs. E. Stresemann, M. J. Tekke, M. Tiedemann, Mrs. M. Tiedemann, W. E. Clyde Todd, N. v. Transehe, J. Van Tyne, C. Wells.

25th June–1st July: Sálim Ali, D. Burckhardt, R. De Laveleye, Miss E. Forster, F. Gudmundsson, Miss S. Knecht, D. Lack, Mrs. D. Lack, L.-W. Masch, Mrs. L.-W. Masch, J. Mills, G. J. van Oordt, C. M. Poulsen, L. Sargent, Mrs. L. Sargent, A. Schifferli, P. Scott, A. Stochholm-Dyhrberg, Miss P. Talbot-Ponsonby, C.Tillisch, E. Tobiesen, Mrs. E. Tobiesen, Miss I. Werth, W. Vogt, Mrs. W. Vogt, G. A. de Vries.

Shorter visits were paid by R. C. Murphy, Mrs. R. C. Murphy, F. Salomonsen, D. Sergeant and M. v. Udvardy.

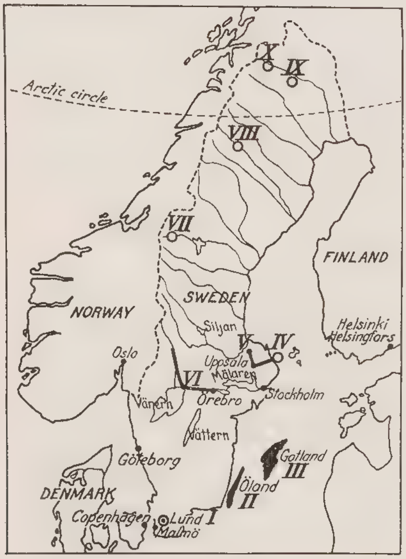
The guides were Elis Wide, C.-F. Lundevall and N.-A. Nilsson.

Abisko Turiststation, where everybody was provided with accommodation, lies on the southern side of the great mountain lake Torneträsk (342 m. s. m.). Foliation of the trees occurred at Abisko in 1950 between the 15th and 20th of June and at Riksgränsen (on the Norwegian frontier) from the 22nd to the 25th of June. On the 18th of June there was still some ice on the north west part of Lake Torneträsk and most of the lakes at higher levels were covered with ice. There was a considerable depth of snow in the mountains at Riksgränsen.

South of Abisko Turiststation there is a valley covered with birch woods, crossed by morainic ridges and with numerous small lakes as well as marshes and bogs. The nearest mountain is Nuolja (1 163 m). The upper limit of the birch-forest ranges from 620 to 750 m. The above-mentioned valley is bounded on the south and south-east by a row of mountains (1 500–1 750 m) with the clearly marked pass Lapporten (the Lapps' Gateway). Excursions were made every day in these areas. Trips were also made to Stordalen east of Abisko, to the barren lands west of Nuolja round Lake Vassijaure, such as the desolate Kärkevagge Valley, as well as to the mountains at Riksgränsen. The slopes on the northern side of Lake Torneträsk were also visited during an excursion by boat.

*Sven Hörstadius.*

## Birds observed during the excursions



The birds which were observed during the excursions are marked with an × in the table. The numbers of the columns correspond to the numbers on the map.

I. Excursions from Lund, Skåne.
II. Excursions on Öland.
III. Excursions on Gotland.
IV. Archipelago excursion from Uppsala.
V. Forest excursion from Uppsala.
VI. Excursion in Närke and Värmland.
VII. Excursions to Handöl, Jämtland.
VIII. Excursion to Ammarnäs, Lappland.
IX. Excursions to Kiruna, Lappland.
X. Excursions to Abisko, Lappland.

## Table of birds observed during the excursions

| | I | II | III | IV | V | VI | VII | VIII | IX | X |
|---|---|---|---|---|---|---|---|---|---|---|
| *Corvus corax* | | | | | | | × | × | × | × |
| *Corvus corone* | × | × | × | × | × | × | × | × | × | × |
| *Corvus frugilegus* | × | × | | | | | | | | |
| *Corvus monedula* | × | × | × | × | × | × | | | | |
| *Pica pica* | × | × | × | × | × | × | × | × | × | × |
| *Nucifraga caryocatactes* | | | | × | × | | | | | |
| *Garrulus glandarius* | | × | × | | × | | | × | | |
| *Cractes infaustus* | | | | | | | × | × | × | |
| *Sturnus vulgaris* | × | × | × | × | × | × | × | × | | × |
| *Chloris chloris* | × | × | × | | × | × | | | | |
| *Carduelis carduelis* | | × | | | | | | | | × |
| *Carduelis spinus* | | | | | × | | × | × | × | |
| *Carduelis flammea* | | | | | | | × | × | × | × |
| *Carduelis hornemanni* | | | | | | | | | | × |
| *Carduelis cannabina* | × | × | × | | × | × | | | | |
| *Pyrrhula pyrrhula* | | | | | × | × | × | × | × | × |
| *Pinicola enucleator* | | | | | | | | × | × | |
| *Loxia curvirostra* | | | | | | | | sp. ? | × | sp. ? |
| *Loxia pytyopsittacus* | | | | | | × | | | | |
| *Loxia leucoptera* | | | | | | | | × | × | |
| *Fringilla coelebs* | × | × | × | × | × | × | × | × | × | × |
| *Fringilla montifringilla* | | | | | | × | × | × | × | × |
| *Emberiza citrinella* | × | × | × | × | × | × | × | × | × | |
| *Emberiza hortulana* | × | | | | | × | | × | | |
| *Emberiza rustica* | | | | | | | | × | × | |
| *Emberiza schoeniclus* | × | × | × | | × | × | × | × | × | × |
| *Calcarius lapponicus* | | | | | | | | × | | × |
| *Plectrophenax nivalis* | | | | | | | × | × | | × |
| *Passer domesticus* | × | × | × | × | × | × | × | | | × |
| *Passer montanus* | × | × | × | × | × | × | | | | |
| *Lullula arborea* | | × | | | × | | | | | |
| *Alauda arvensis* | × | × | × | × | × | × | | | | |
| *Eremophila alpestris* | | | | | | | | × | × | × |
| *Anthus campestris* | × | | × | | | | | | | |
| *Anthus trivialis* | × | × | | × | × | × | × | × | × | × |
| *Anthus pratensis* | × | × | × | | × | × | × | × | × | × |
| *Anthus cervinus* | | | | | | | | | | × |
| *Anthus spinoletta* | | | × | | | | | | | |
| *Motacilla flava* | × | × | × | | × | × | × | × | × | × |
| *Motacilla alba* | × | × | × | × | × | × | × | × | × | × |
| *Certhia familiaris* | | × | × | | × | × | | × | | |

| | I | II | III | IV | V | VI | VII | VIII | IX | X |
|---|---|---|---|---|---|---|---|---|---|---|
| *Sitta europaea* | | × | × | | × | | | | | |
| *Parus major* | × | × | × | × | × | × | × | × | × | × |
| *Parus caeruleus* | × | × | × | | × | × | | | | |
| *Parus ater* | | | × | | × | × | | × | | |
| *Parus cristatus* | | | | | × | × | | | | |
| *Parus cinctus* | | | | | | | | | × | × |
| *Parus palustris* | | × | | | × | × | | | | |
| *Parus atricapillus* | | | | | × | × | × | × | × | × |
| *Aegithalos caudatus* | | × | | | × | | | | | |
| *Lanius excubitor* | | | | | | | × | × | | × |
| *Lanius collurio* | × | × | × | | × | × | | | | |
| *Bombycilla garrulus* | | | | | | | | | × | × |
| *Muscicapa striata* | × | × | × | | × | × | × | × | × | × |
| *Muscicapa hypoleuca* | × | × | × | × | × | × | × | × | × | × |
| *Muscicapa albicollis* | | | × | | | | | | | |
| *Muscicapa parva* | | × | | | | | | | | |
| *Regulus regulus* | × | | | | × | × | × | × | | |
| *Phylloscopus collybita* | | | | | | × | | | | |
| *Phylloscopus trochilus* | × | × | × | × | × | × | × | × | × | × |
| *Phylloscopus sibilatrix* | × | × | × | | × | × | | | | |
| *Phylloscopus borealis* | | | | | | | | | | × |
| *Locustella fluviatilis* | | | | | | × | | | | |
| *Acrocephalus scirpaceus* | × | × | | | × | × | | | | |
| *Acrocephalus schoenobaenus* | × | × | × | | × | × | | | | × |
| *Hippolais icterina* | × | × | × | | | × | × | | | |
| *Sylvia nisoria* | | × | | | | | | | | |
| *Sylvia borin* | × | × | × | × | × | × | × | × | | × |
| *Sylvia atricapilla* | × | × | | | × | × | × | | | |
| *Sylvia communis* | | × | × | | × | × | | | | |
| *Sylvia curruca* | | × | × | | × | × | × | × | | |
| *Turdus pilaris* | | | × | × | × | × | × | × | × | × |
| *Turdus viscivorus* | | | × | | × | × | | | × | |
| *Turdus ericetorum* | × | × | × | | × | × | × | × | × | × |
| *Turdus musicus* | | | | | × | × | × | × | × | × |
| *Turdus torquatus* | | | | | | | × | × | | × |
| *Turdus merula* | × | × | × | × | × | × | | | | |
| *Oenanthe oenanthe* | × | × | × | × | × | × | × | × | × | × |
| *Saxicola rubetra* | × | × | × | | × | × | | × | × | × |
| *Phoenicurus phoenicurus* | × | × | × | | × | × | × | × | × | × |
| *Luscinia luscinia* | × | × | | | | | | | | |
| *Luscinia svecica* | | | | | | | × | × | | × |
| *Erithacus rubecula* | × | × | × | × | × | × | × | × | × | |
| *Prunella modularis* | | | | | × | × | × | × | × | × |
| *Troglodytes troglodytes* | | | | | × | × | | × | | |
| *Cinclus cinclus* | | | | | | | × | × | | × |

| | I | II | III | IV | V | VI | VII | VIII | IX | X |
|---|---|---|---|---|---|---|---|---|---|---|
| *Hirundo rustica* | × | × | × | × | × | × | | × | | × |
| *Delichon urbica* | × | × | × | × | × | × | × | × | × | × |
| *Riparia riparia* | | × | | | × | × | × | × | × | × |
| *Apus apus* | × | × | × | × | × | × | | × | × | × |
| *Caprimulgus europaeus* | | | × | | × | × | | | | |
| *Coracias garrulus* | | | × | | | | | | | |
| *Alcedo atthis* | | | | | | × | | | | |
| *Picus viridis* | | × | | | × | × | | | | |
| *Dendrocopos major* | × | × | | | × | | | | | |
| *Dendrocopos minor* | | | × | | | | | | | |
| *Picoides tridactylus* | | | | | | | × | × | | × |
| *Dryocopus martius* | | | × | | × | | | | | |
| *Jynx torquilla* | | × | × | | × | × | | | | |
| *Cuculus canorus* | × | × | × | | × | × | × | × | × | × |
| *Surnia ulula* | | | | | | | | × | × | |
| *Glaucidium passerinum* | | | | | × | | | | | |
| *Aegolius funereus* | | | | | × | | × | | | |
| *Asio flammeus* | | | | | | | | | | × |
| *Strix aluco* | | × | | | × | × | | | | |
| *Falco rusticolus* | | | | | | | | | | × |
| *Falco peregrinus* | | × | | | | | | | | |
| *Falco subbuteo* | × | × | × | | × | × | | | | |
| *Falco columbarius* | | | × | | | × | × | × | × | × |
| *Falco tinnunculus* | × | × | × | | | | | × | × | × |
| *Aquila chrysaëtos* | | | | | | dead | | × | × | |
| *Buteo lagopus* | | | | | | | × | × | × | × |
| *Buteo buteo* | × | × | | | × | × | | × | | |
| *Circus aeruginosus* | × | × | | | | × | | | | |
| *Circus pygargus* | | × | | | | | | | | |
| *Circus cyaneus* | | | | | | | × | × | × | |
| *Accipiter gentilis* | | | | | × | × | | | | × |
| *Accipiter nisus* | | × | | | × | | × | | × | |
| *Milvus milvus* | × | | | | | | | | | |
| *Haliaeetus albicilla* | | | | × | × | | | | × | × |
| *Pernis apivorus* | × | | | × | × | × | | | × | |
| *Pandion haliaëtus* | | | | × | × | × | | × | | |
| *Ciconia ciconia* | × | | | | | | | | | |
| *Ardea cinerea* | × | × | | | | | | | | |
| *Cygnus cygnus* | | × | | | | | | | × | |
| *Cygnus olor* | × | × | | × | × | × | | | | |
| *Anser erythropus* | | | | | | | | × | | × |
| *Anser fabalis* | | | | | | | | | × | sp.? |
| *Branta bernicla* | | × | | | | | | | | |
| *Tadorna tadorna* | | × | × | | | | | | | |
| *Anas platyrhynchos* | × | × | × | × | × | × | × | × | × | × |

| | I | II | III | IV | V | VI | VII | VIII | IX | X |
|---|---|---|---|---|---|---|---|---|---|---|
| *Anas crecca* | × | × | × | | × | × | × | × | × | × |
| *Anas querquedula* | × | × | | | | | | × | | |
| *Anas penelope* | | × | | | | | × | × | × | × |
| *Anas acuta* | × | × | × | | | | × | × | | × |
| *Anas clypeata* | × | × | × | | × | × | | | | |
| *Aythya ferina* | × | × | × | | × | | | | | |
| *Aythya fuligula* | | × | × | × | × | × | | × | × | × |
| *Aythya marila* | | × | | | | | × | × | | × |
| *Bucephala clangula* | | | | | × | × | × | × | × | × |
| *Clangula hyemalis* | | | | | | | × | | | × |
| *Somateria mollissima* | × | × | × | × | | | | | | |
| *Melanitta nigra* | | × | | | | | × | × | × | × |
| *Melanitta fusca* | | × | × | × | | | × | × | × | × |
| *Mergus merganser* | | | | × | | × | × | × | × | |
| *Mergus serrator* | × | × | × | × | | × | × | | × | × |
| *Phalacrocorax carbo* | | | | | | | | | | × |
| *Podiceps cristatus* | × | | | × | × | × | | | | |
| *Podiceps auritus* | | × | × | | × | | | | | |
| *Colymbus arcticus* | | | | | × | × | × | × | × | × |
| *Colymbus stellatus* | | | × | | | × | × | | × | × |
| *Columba palumbus* | × | × | × | × | × | × | | | | |
| *Columba oenas* | × | × | × | | × | | | | | |
| *Limosa limosa* | | × | × | | | | | | | |
| *Numenius arquata* | × | × | × | | × | × | × | | | |
| *Numenius phaeopus* | | | | | | | × | × | × | × |
| *Scolopax rusticola* | | × | × | | × | × | × | × | | |
| *Capella media* | | | | | | | | × | | × |
| *Capella gallinago* | × | × | × | | × | × | × | × | | × |
| *Lymnocryptes minimus* | | | | | | | | | | × |
| *Phalaropus lobatus* | | × | | | | | × | × | | × |
| *Arenaria interpres* | | × | × | | | | | | | |
| *Calidris alpina* | × | × | | | | | | × | | |
| *Calidris ferruginea* | | × | | | | | | | | |
| *Calidris temminckii* | | | | | | | × | × | | × |
| *Calidris maritima* | | | | | | | × | × | | × |
| *Philomachus pugnax* | × | × | × | | | | × | × | | × |
| *Limicola falcinellus* | | | | | | | | × | | × |
| *Tringa hypoleucos* | | | | | × | × | × | × | × | × |
| *Tringa glareola* | | | | | × | × | × | × | × | × |
| *Tringa ochropus* | | | | | × | × | × | | × | |
| *Tringa totanus* | × | × | × | × | | | × | | | × |
| *Tringa erythropus* | | × | × | | | × | | × | × | × |
| *Tringa nebularia* | | | | | | | × | × | × | × |
| *Charadrius hiaticula* | × | × | × | × | | | × | × | | × |
| *Charadrius dubius* | | | × | | | × | | | | |

| | I | II | III | IV | V | VI | VII | VIII | IX | X |
|---|---|---|---|---|---|---|---|---|---|---|
| *Charadrius alexandrinus* | × | × | | | | | | | | |
| *Charadrius morinellus* | | | | | | | × | × | | × |
| *Pluvialis apricaria* | | × | | | | × | × | × | × | × |
| *Pluvialis squatarola* | | × | | | | | | | | |
| *Vanellus vanellus* | × | × | × | × | × | × | | | | |
| *Recurvirostra avosetta* | × | × | | | | | | | | |
| *Haematopus ostralegus* | × | × | × | × | | | | | | |
| *Grus grus* | × | × | | | × | | × | | × | |
| *Chlidonias niger* | × | × | | | | | | | | |
| *Hydroprogne tschegrava* | | × | × | × | | | | | | |
| *Sterna sandvicensis* | × | × | | | | | | | | |
| *Sterna hirundo* | × | × | × | × | | × | | | | |
| *Sterna paradisaea* | × | × | × | × | | | × | × | | × |
| *Sterna albifrons* | × | × | × | | | | | | | |
| *Larus minutus* | | × | × | | | | | | | |
| *Larus ridibundus* | × | × | × | | × | × | × | | | |
| *Larus canus* | | × | × | × | × | × | × | × | | × |
| *Larus argentatus* | × | × | × | × | | × | | | | × |
| *Larus fuscus* | | × | × | × | | | | | | × |
| *Larus marinus* | × | × | × | | | | | | | |
| *Stercorarius parasiticus* | | | | × | | | | | | |
| *Stercorarius longicaudus* | | | | | | | | × | | × |
| *Alca torda* | | | × | | | | | | | |
| *Uria aalge* | | × | × | | | | | | | |
| *Uria grylle* | | × | × | × | | | | | | |
| *Crex crex* | | × | × | | | | | | | |
| *Porzana porzana* | | | | | × | × | | | | |
| *Rallus aquaticus* | | × | | | × | | | | | |
| *Gallinula chloropus* | × | × | | | × | × | | | | |
| *Fulica atra* | × | × | × | × | × | × | | | | |
| *Tetrao urogallus* | | | | × | × | × | × | × | × | × |
| *Lyrurus tetrix* | | × | | | × | | × | × | × | × |
| *Lagopus lagopus* | | | | | | | × | × | × | × |
| *Lagopus mutus* | | | | | | | × | × | | × |
| *Tetrastes bonasia* | | | | | × | × | × | | | |
| *Perdix perdix* | | × | | | | | | | | |
| *Phasianus colchicus* | | | × | | × | × | | | | |

## Programme

**Saturday, June 10**

3 p.m. Congress Hall.

Opening of the Congress by the President, Dr. A. Wetmore.

Presidential address: Recent additions to our knowledge of Prehistoric Birds, 1933—1949.

S. Hörstadius: Introduction to Swedish ornithology.

P. O. Swanberg: Food storage, territory, and song in the Thick-billed Nutcracker (*Nucifraga c. caryocatactes*).

B. Haglund: Colourfilm on Swedish Wild Life.

**Sunday, June 11**

Excursion to the Norrtälje archipelago.

**Monday, June 12**

9 a.m. Congress Hall.

EVOLUTION AND SYSTEMATICS

Chairman: N. Gyldenstolpe. Secretary: W. H. Phelps, Jr.

E. Mayr: Bird speciation. Paper read by Dr. R. Murphy. 45 min.

E. Stresemann: Der Einfluss philosophischer Naturbetrachtung auf die ornithologische Systematik. 20 min.

D. Amadon: Evolution of the Hawaiian Honey-creepers (Family Drepaniidae). 20 min.

W. B. Yapp: Ecological speciation in the genus Phylloscopus. 10 min.

R. Meinertzhagen: Desert colouration. 20 min.

2 p.m. Congress Hall.

BIRD MIGRATION AND ORIENTATION

Chairman: H. Noll. Secretary: B. Løppenthin.

R. Drost: Bird Migration. 45 min.

A. Landsborough Thomson: Breeding seasons, migration, and moult: factors controlling the annual cycle. 10 min.

G. Rudebeck: Some notable factors concerning the migration of palaearctic birds. 30 min.

R. E. Moreau: Migration system in perspective. 10 min.

E. Schüz: Ergebnisse der Orientierungsversuche der Vogelwarte Rossitten. 20 min.

7 p.m. University lecture room nr. X.

## FILMS

Chairman: G. C. A. Junge.

R. B. Sibson: The recently rediscovered Takahe (*Notornis*). Film by Dr. R. A. Falla.

P. Scott: The researches of the Severn Wildfowl Trust. Wild and tame Anatidae at the Severn Research Station. 25 min.

S. Dillon Ripley: Short communication on the avifauna of Nepal, in connection with a film from Nepal. 75 min.

**Tuesday, June 13**

9 a.m. Congress Hall.

## BIRD BEHAVIOUR

Chairman: P. Jespersen. Secretary: E. Merikallio.

N. Tinbergen: Report on recent advances in the study of bird behaviour. 45 min.

E. Fabricius: Some experiments on inprinting phenomena in ducks. 15 min.

D. Lack: Colour film of Robin display. 2 min.

H. Poulsen: Inheritance and learning in the song of the Chaffinch, *Fringilla coelebs* L., and a colourfilm: Display of the Shoe-Billed Heron, *Balæniceps rex* J. Gd., and the Condor, *Vultur gryphus* L. 20 min.

G. Kramer: Die Balz des Rotrückenwürgers. Mit Aufnahmen von Ursula v. St.-Paul. 10 min.

D. Burckhardt: The display of the Satin Bowerbird, *Ptilonorhynchus violaceus*. With film and sound record. 10 min.

F. Steiniger: Tierpsychologische Gesichtspunkte bei der Photographie freilebender Vögel. 15 min.

2 p.m. Congress Hall.

### POPULATION DYNAMICS

Chairman: H. Lloyd. Secretary: R. E. Moreau.

D. Lack: Population ecology. 45 min.

J. Fisher: The present population of the North Atlantic Gannet (*Sula bassana*). 7 min.

R. C. Murphy: A population study of the wedge-tailed shearwater (*Puffinus pacificus*). 10 min.

I. Välikangas: Invasion von *Phylloscopus trochiloides viridanus* Blyth über den Finnischen Meerbusen nach Norden. 20 min.

G. Svärdson and S. Durango: Spring weather and population fluctuations. 10 min.

7 p.m. University lecture room nr. X.

### FILMS

Chairman: J. S. Huxley.

A. A. Allen: The Curlew's secret. 25 min.

W. E. Clyde Todd: Birds of Northern Ungava. 30 min.

W. H. Bierman: Whales and birds observed during the first Dutch Whaling Expedition to the Antarctic. 30 min.

I. Homoki Nagy: Colour slides of Hungarian birds.

**Wednesday, June 14**

Excursion by bus to a coniferous forest region and a fen district north of Uppsala.

**Thursday, June 15**

9 a.m. University lecture room nr. X.

### MIGRATION AND ORIENTATION (continued)

Chairman: E. Schüz. Secretary: A. Schifferli.

A. M. Hemmingsen: The relation of bird migration in North Eastern China to body weight and its bearing on Bergmann's rule. 10 min.

V. Olsson: Ottenby Bird Station. 30 min.

R. B. Sibson: Some aspects of bird migration in New Zealand. 12 min.

A. Van Beneden: La migration d'août en Belgique. 10 min.

P. Jespersen: Contribution à la connaissance de la migration des Cigognes blanches en Afrique du Nord. 10 min.

G. Bouet: Les Cigognes blanches de l'Afrique du Nord et leur migration. 10 min. Paper read by J. Berlioz.

A. M. Hemmingsen: Observations on the migration of the Eastern White Stork (*Ciconia ciconia boyciana* Swinhoe). 5 min.

9 a.m. University lecture room nr. IX.

### ECOLOGY OF CERTAIN SPECIES

Chairman: D. Lack. Secretary: J. Dorst.

D. Sergeant: Ecological relationships of the two Guillemots *Uria aalge* and *Uria lomvia*. 15 min.

D. Amadon: Madagascar's Pseudo-sunbird. 10 min.

J. Van Tyne: The distribution of the Kirtland Warbler (*Dendroica kirtlandii*). 20 min.

Miss V. Maxse: *Aegithalos caudatus roseus*. How its nest is built. 10 min.

H. R. Tutt: Data on the excavation of the nest-hole and feeding of the young of the Green Woodpecker (*Picus viridis*). 20 min.

H. Noll: Der Rhythmus in den Brutzeiten einiger schweizerischer Vögel. 10 min.

E. J. L. Hallstrom: The Black Cockatoo. 45 min.

2 p.m. University lecture room nr. X.

### MIGRATION AND ORIENTATION (continued)

Chairman: G. Svärdson. Secretary: G. Rudebeck.

G. Rudebeck: The migration of the birds of prey in Southern Sweden. 30 min.

T. Malmberg: Bird migration in NW Scania. 10 min.

J. Berry: On the emigration to North Norway of Barnacle Geese (*Branta leucopsis*), which had been bred in Scotland. 5 min.

G. Svärdson: Swift movements in summer. 10 min.

R. Hylbom: Daily ringing figures and passing frequency in small Passerines. 10 min.

H. Johansen: Über die Vogelberingungsarbeit des Zoologischen Museums in Kopenhagen. 15 min.

A. M. Hemmingsen: The relation of spring migration to day length and solar radiation. 5 min.

G. Kramer: Eine neue Methode zur Erforschung der Zugorientierung und die ersten Ergebnisse. 30 min.

2 p.m. University lecture room nr. IX.

### PALAEONTOLOGY, ANATOMY, AND VARIOUS TOPICS

Chairman: L. de Beaufort. Secretary: F. Salomonsen.

R. C. Murphy: The moa deposits of Pyramid Valley Swamp, New Zealand. 15 min.

A. Kleinschmidt: Eine Rekonstruktion des Schädels des *Archaeornis siemensi* Dames (mit Demonstration). 10 min.

K. G. Wingstrand: The structures in the avian pituitary responsible for the transfer of stimuli from the nervous to the hormonal system. 20 min.

E. Sutter: Wachstum und Differenzierung des Gehirns bei Nestflüchtern und Nesthockern. 20 min.

E. van Koersfeld: Difficulties with stomach-analysis. 5 min.

R. Spärck: Food of North European gulls. 10 min.

Fräulein S. Knecht: Gesang, Gehör und Musikalität der Vögel. 10 min.

M. v. Udvardy: Heat resistance in birds. 10 min.

A. Kleinschmidt: Das Flugvermögen der seglerartigen Vögel (Macropterygidae). 15 min.

7 p.m. University lecture room nr. X.

### FILMS

Chairman: J. Berlioz.

N. Tinbergen: Experimental analysis of stimuli releasing the begging response in Herring Gull chicks. 40 min.

L. S. Crandall: Afropavo in captivity, and displays of *Agriocharis, Cephalopterus* and *Procnias tricarunculata*. 10 min.

O. Koehler: Vögel erlernen unbenannte Anzahlen. Paper 15 min., film 30 min.

H. Dirkx: *Ixobrychus minutus* and *Locustella luscinioides*. 15 min.

**Friday, June 16**

9 a.m. University lecture room nr. X.

### EVOLUTION AND SYSTEMATICS (continued)

Chairman: Sir Norman Kinnear. Secretary: S. Durango.

K. H. Voous: Distributional and evolutionary history of the Kingfisher genus *Ceyx* in Malaysia. 18 min.

J. M. Harrison: On some phylogenetic trends in *Garrulus glandarius* and *Dendrocopus major*. 15 min.

Mrs. E. G. Allen: A sixteenth century system of classification. 10 min.

F. Salomonsen: The genus-name Colymbus. The nomenclature controversy. 10 min.

A. Ghigi: Nomenclature, genetics and classification in Guinea-Fowls. 10 min.

C. Vaurie: Preliminary results from the Koelz Asiatic Collections. 10 min.

R. A. H. Coombes: Races of the Bean Goose (*Anser fabalis*) in Western Europe. 5 min.

C. Jouanin: Remarques sur les Cormorans de la région australe americaine. 10 min.

J. Dorst: Systématique des Turdidés. 10 min.

9 a.m. University lecture room nr. IX.

### REGIONAL FAUNAS

Chairman: Sálim Ali. Secretary: G. Kramer.

H. Holgersen: Avifauna of the antarctic Peter I Island. 10 min.

B. Løppenthin: Sea Birds of the Persian Gulf. 20 min.

A. Schifferli: Vom Brutvogelbestand in einem Hochgebirgswald des Wallis. 10 min.

E. Nicholson: Birds of the North Atlantic. 10 min.

Y. Hagen: Birds of Tristan da Cunha. 20 min.

P. Scott: Birds in the Canadian Arctic. With film: Birds of the Canadian Arctic in the summer. 65 min.

9 a.m. University lecture room nr. IV.

### ROUND TABLE CONFERENCE ON BIRD RINGING

Chairmen: F. C. Lincoln and A. Landsborough Thomson.
Secretaries: Mrs. D. Lack and A. Schifferli.

2 p.m. University lecture room nr. X.

### POPULATION DYNAMICS (continued)

Chairman: R. C. Murphy. Secretary: K. Voous.

J. Fisher: The changes in the distribution of the Fulmar (*Fulmarus glacialis*). 20 min.

J. Peitzmeier: Beobachtungen über Klimaveränderungen und Bestandsveränderungen einiger Vogelarten in Nordwestdeutschland. 15 min.

F. Salomonsen: The immigration and breeding of the Fieldfare (*Turdus pilaris* L.) in Greenland. 15 min.

F. Gudmundsson: The effects of the recent climatic changes on the bird life of Iceland. 25 min.

E. Merikallio: Über die Einwirkung der letzten Wärmeperiode (1930–1949) auf die Vogelfauna des nördlichen Finlands. 30 min.

P. Grenquist: Statistical notes on the recent fluctuations in number of waterfowl in the Finnish archipelago. 10 min.

A. Keve and M. v. Udvardy: Increase and decrease of the breeding range of some birds in Hungary. 10 min.

A. O. Gross: Control of the Herring Gull (*Larus argentatus smithsonianus*) and the Cormorant (*Phalacrocorax auritus auritus*) on the New England coast, U. S. A. With film.

As the times in this section were considerably exceeded the papers by E. Merikallio, P. Grenquist, M. v. Udvardy and A. O. Gross had to be presented on Saturday morning in lecture room nr. X.

2 p.m. University lecture room nr. IV.

ROUND TABLE CONFERENCE ON BIRD RINGING (continued)

Chairmen: F. C. Lincoln and A. Landsborough Thomson.
Secretaries: Mrs. D. Lack and A. Schifferli.

4—5 p.m. excursion by bus to *Gamla Uppsala*, where tea was served, and to *Linnés Hammarby*. Back in Uppsala 6—7 p.m.

8 p.m. in the hall of Vasa Castle CONGRESS DINNER, presided over by His Excellency The Governor of the Province of Uppsala, Mr. H. Kjellman, and offered by Sveriges Ornitologiska Förening (Swedish Ornithological Association). Morning dress.

**Saturday, June 17**

9 a.m. Congress Hall.

Chairman: A. Wetmore. Secretary: S. Hörstadius.

Mrs. G. E. B. Murphy: Conservation in ornithological programs. 10 min.

R. Kuhk: Zur Mitarbeit nichtfachlicher Kräfte in der Ornithologie. 10 min.

Miss T. Clay: The Mallophaga as an aid to the classification of birds with special reference to feather structure. 20 min.

A. A. Allen: Recent advances in bird photography and sound recording. With sound records and slides. 20 min.

D. Lack: The Galapagos Finches. With film. 7 min.

W. Vogt: Ecology of the Peruvian Guano Islands. With film. 35 min.

Closing of the Congress.

## Delegates
## Institutions and Societies Represented

*Argentina*

Instituto Miguel Lillo, Tucumán: C. G. Olrog

*Australia*

Royal Zoological Society of New South Wales, Sydney: W. R. Moore, E. J. L. Hallstrom
Taronga Zoological Park Trust, Sydney: E. J. L. Hallstrom

*Austria*

The Government: Dr. M. Sassi
Museum of Natural History: Dr. M. Sassi

*Belgium*

Institut Royal des Sciences Naturelles, Bruxelles: Dr. R. Verheyen

*Canada*

National Museum of Canada, Ottawa: Hoyes Lloyd
Wildlife Division, Department of Resources and Development, Ottawa: Hoyes Lloyd

*Colombia*

Instituto de Ciencias Naturales, Bogotá: William H. Phelps

*Denmark*

Dansk Ornithologisk Forening, Copenhagen: Dr. P. Jespersen
Universitetets Zoologiske Museum, Copenhagen: Prof. R. Spärck, Dr. F. Salomonsen

*Finland*

Academia Scientiarum Fennica, Helsinki: Prof. I. Välikangas
Finlands Ornithologiska Förening, Helsinki: Dr. O. Kalela
Universitetets Zoologiska Museum, Helsinki: Dr. O. Kalela

*France*

Museum National d'Histoire Naturelle, Paris: Prof. J. Berlioz
Société National d'Acclimatation, Paris: Dr. J. Dorst, Dr. G. Thibout
Société Ornithologique de France, Paris: P. Engelbach, R. Etchécopar, G. Olivier

*Great Britain*

Avicultural Society, London: Miss P. Barclay-Smith
Birmingham and West Midland Bird Club: Miss C. K. James

British Association for the Advancement of Science, London: Dr. E. Hindle
British Museum (Natural History), London: Sir Norman Kinnear
British Ornithologists' Union, London: Dr. A. Landsborough Thomson, Miss P. Barclay-Smith
British Trust of Ornithology: E. M. Nicholson
Cornwall Bird Watching and Preservation Society: A. G. Parsons
International Wildfowl Research Institute: R. A. H. Coombes
Natural History Society of Northumberland, Durham and Newcastle upon Tyne, Newcastle: Miss G. Watt
The Royal Society, London: Dr. E. Hindle, Dr. J. S. Huxley, Dr. D. Lack
The Royal Society of Edinburgh: Dr. J. Berry
Royal Society for the Protection of Birds: R. Preston Donaldson, E. Cohen, J. Fisher
Scottish Ornithologists' Club: Miss E. V. Baxter
Society for Promotion of Nature Reserves: Dr. H. Smith
Zoological Society of London: Sir Norman Kinnear

### *Germany*

Deutsche Ornithologische Gesellschaft: Prof. E. Stresemann, Dr. L. Schuster, Dr. R. Kuhk
Humboldt-Universität, Berlin: Prof. E. Stresemann
Staatliches Museum für Naturkunde, Stuttgart: Dr. E. Schüz
Staatliches Naturhistorisches Museum, Braunschweig: Dr. Adolf Kleinschmidt
Staatliche Vogelwarte Helgoland, Sitz Wilhelmshaven: Prof. R. Drost
Zoologisches Forschungsinstitut und Museum Al. Koenig, Bonn: Dr. A. von Jordans

### *Iceland*

Museum of Natural History, Reykjavik: Dr. F. Gudmundsson

### *India*

Bombay Natural History Society: Sálim Ali

### *Italy*

Research Council of the Government: Prof. A. Ghigi, Prof. A. Toschi

### *Luxembourg*

The Government: A. Van Beneden, Belgium

### *Netherlands*

Club van Nederlandsche Vogelkundigen: W. Ph. Hellebrekers, J. G. van Marle
Nederlandsche Ornithologische Vereeniging: Prof. L. F. de Beaufort, Dr. K. H. Voous
Rijksmuseum van Naturlijke Historie: Dr. G. C. A. Junge

### *Norway*

Stavanger Museum, Stavanger: H. Holgersen

*New Zealand*

Avicultural Society: Miss P. Barclay-Smith
Ornithological Society: R. B. Sibson

*Sweden*

Malmö Museum, Malmö: H. Bergman
Naturhistoriska Museet, Göteborg: V. Fontaine, J. Lepiksaar
Naturhistoriska Riksmuseet, Stockholm: Dr. N. Gyldenstolpe
Zoologiska Institutionen, Lund: G. Rudebeck

*United States of America*

U. S. Official Delegation: Dr. A. Wetmore, H. Friedmann, A. O. Gross, F. C. Lincoln, D. Ripley, J. Van Tyne
Academy of Natural Sciences, Philadelphia: Dr. A. Wetmore
American Ornithologists' Union: Dr. R. C. Murphy, Dr. A. Wetmore
American Museum of Natural History, New York: Dr. R. C. Murphy
American Philosophical Society, Philadelphia: Dr. A. Wetmore
American Society of Naturalists: Dr. Ernst Mayr
Carnegie Museum, Pittsburgh: W. E. Clyde Todd
Cooper Ornithological Club, Berkeley: Mrs. J. Kelly
Laboratory of Ornithology, Cornell University, Ithaca N. Y.: Prof. A. A. Allen
National Academy of Sciences, Washington: Dr. A. Wetmore
National Audubon Society, New York: R. T. Peterson
New York Zoological Society, New York: L. S. Crandall
Smithsonian Institution, Washington: Dr. A. Wetmore
Society of Women Geographers': Mrs. Grace E. Barstow Murphy, Mrs. E. M. B. Naumburg
University of Kansas: Dr. A. Wetmore
University of Michigan, Museum of Zoology, Ann Arbor: J. Van Tyne
U.S. Department of Interior, Fish and Wildlife Service: F. C. Lincoln, A. O. Gross
U.S. National Museum, Washington: Dr. H. Friedmann

## Members of the Congress

* Registered, but not in attendance
( ) Present only on excursions

Acland, C.; Miss, Banstead, England
Adelholt, E.; Miss, Copenhagen, Denmark
Adelsköld, E.; Uppsala, Sweden
Ali, Sálim; Bombay, India
Allen, A. A.; Prof., Ithaca N. Y., U. S. A.
Allen, E. G.; Mrs., Ithaca N. Y., U. S. A.
Amadon, D.; Dr., New York, U. S. A.
Appelman, F. J.; Dr., Den Haag, Holland
Armitage, P.; Miss, Headington Oxford, England
Armington, S.; Stockholm, Sweden
Bailey, F. M.; Northrepps, England
Banér, S.; Hjälstaby, Sweden
Barclay-Smith, P.; Miss, London, England
*Barlow, T.; Wendover, England
Barrington, F. J. F.; London, England
Barrington, J.; Dublin, N. Ireland
Baxter, E.; Miss, Upper Largo Fife, Scotland
de Beaufort, L.; Prof., Amsterdam, Holland
de Beaufort, J.; Mrs., Amsterdam, Holland
Benzon, B.; Dr., Springforbi, Denmark
Bergman, H.; Dr., Malmö, Sweden
Bergman, S.; Rönninge, Sweden
Bergström, U.; Stocksund, Sweden
Berlioz, J.; Prof., Paris, France
Berry, J.; Dr., Edinburgh, Scotland
Bertelsen, E.; Miss, Århus, Denmark
*Berthet, G.; Lyon, France
*Berthet, R.; Mrs., Lyon, France
Berzins, B.; Lund, Sweden (formerly in Latvia)
Bierman, W. H.; Dr.,Haarlem, Holland
Blatter, F.: Dr., Bern, Switzerland
Blatter, F.; Mrs., Bern, Switzerland
Blume, C.; Copenhagen, Denmark
Bodman, N. v. u. z.; Möggingen ü. Radolfzell, Germany
*Börjesson, E.; Göteborg, Sweden
*Bouet, G.; Dr., Paris, France
Broberg, G.; Strängnäs, Sweden
Brouwer, G.; Bilthoven, Holland
Brouwer, G.; Mrs., Bilthoven, Holland
*Bruyns, M.; Dr., Utrecht, Holland
*Bruyns, M.; Mrs., Utrecht, Holland
Bryson, A.; Edinburgh, Scotland
*Buisman, H. H.; Leeuwarden, Holland
Burckhardt, D.; Basel, Switzerland
van der Burg, R.; De Steeg, Holland
Buttet, G.; Switzerland
Carnes, B.; Mrs., Tenafly, N. J., U. S. A.
Chalif, E.; Short Hills, N. J., U. S. A.
Chalif, E.; Mrs., Short Hills, N. J., U. S. A.
Clay, T.; Miss, London, England
Cohen, E.; Sway, England
Coombes, R. A. H.; Tring, England
Course, H.; Royston, England
Crandall, L.; New York, U. S. A.
Cunningham, J.; Belfast, N. Ireland
Cunningham, J.; Mrs., Belfast, N. Ireland
Cunningham, S.; Belfast, N. Ireland
Curry-Lindahl, K.; Huddinge, Sweden
Dahlbeck, N.; Dr., Stockholm, Sweden
Danielsson, G.; Stockholm, Sweden
Davis, H.; Bristol, England
Delacour, J.; New York, U. S. A.
De Laveleye, R.; Dr., Paris, Belgium

De Maerschalck, J.; Denderbelle, Belgium
*Derscheid, J.; Mme, Brabant, Belgium
de Worms, C.; Woking, England
Dirkx, H.; Antwerp, Belgium
(van Dobben, W.; Dr., Wageningen, Holland)
Donaldson, R. P.; Beckenham, England
Donaldson, R. P.; Mrs., Beckenham, England
Dorst, J.; Dr., Paris, France
Dorst, J.; Mrs., Paris, France
Drost, R.; Prof., Wilhelmshaven, Germany
Durango, S.; Täby, Sweden
Durango, S.; Mrs., Täby, Sweden
Dijkstra, M.; Heemstede, Holland
*Edelstam, C.; Stockholm, Sweden
*Edge, R.; Mrs., New York, U. S. A.
Edmond-Blanc, F.; Neuilly-sur-Seine, France
Ehnberg, M.; Mrs., Lidingö, Sweden
Ekman, S.; Prof., Uppsala, Sweden
Elofson, Olof; Dr., Sundsvall, Sweden
Engelbach, P.; Paris, France
Espana Cantos, J.; Madrid, Spain
Etchécopar, R.; Paris, France
Eygenraam, J. A.; Ede, Holland
Fabricius, E.; Bromma, Sweden
Fabricius, E.; Mrs., Bromma, Sweden
Faxén, L.; Linköping, Sweden
Ferdinand, J.; Tappernöje, Denmark
Ferdinand, L.; Dr., Copenhagen, Denmark
(Feremans, T.; Brussels, Belgium)
Ferrier, J. M.; Miss, Holt, England
Ferry, C.; Dr., Dijon, France
Ferry, C.; Mrs., Dijon, France
Fischer, J. A.; Mrs., De Steeg, Holland
Fisher, J.; Ashton, England
Fitter, R.; Burford, England
Fitter, R.; Mrs., Burford, England
(Flodmark, S.; Lund, Sweden)
Fontaine, V.; Göteborg, Sweden
Forselius, S.; Uppsala, Sweden
Forster, E.; Miss, London, England
Friedmann, H.; Dr., Washington, U. S. A.
Fröhlich, Th.; Copenhagen, Denmark
*Genzmer, G.; Miss, Bremen, Germany
Ghigi, A.; Prof., Bologna, Italy
Giersberg, H.; Prof., Frankfurt a. Main, Germany
Godman, Edith; Miss, Horsham, England
Godman, Eva; Miss, Horsham, England
de Greef, G.; Dr., Flushing, Holland
Grenquist, P.; Helsinki, Finland
Gross, A. O.; Dr., Brunswick, Maine, U. S. A.
Gross, A. O.; Mrs., Brunswick, Maine, U. S. A.
Gudmundsson, F.; Dr., Reykjavik, Iceland
Gunnerbeck, E.; Stockholm, Sweden
Gustafson, R.; Miss, Stockholm, Sweden
Gyldenstolpe, N.; Dr., Stockholm, Sweden
Haftorn, S.; Drammen, Norway
Hagen, Y.; Jeløy, Norway
Hagliden, G.; Örebro, Sweden
Haglund, B.; Stockholm, Sweden
Hallstrom, E. J. L.; Sydney, Australia
Hannerz, D.; Norrtälje, Sweden
Hansen, B. S.; Copenhagen, Denmark
(Hansen, E.; Copenhagen, Denmark)
Harrison, J.; Dr., Sevenoaks, England
*Haverschmidt, F.; Paramaribo, Dutch Guiana
Heath, R.; London, England
Hellebrekers, H.; Delft, Holland
Hellebrekers, W.; Delft, Holland
Helmy, Mohammed; Cairo, Egypt.
Hemmingsen, A.; Dr., Hellerup, Denmark
*Hens, P.; Valkenburg, Holland
Herner, T.; Dr., Lund, Sweden
*Hindle, E.; Dr., London, England
Hoffman, L.; Basel, Switzerland
v. Hofsten, B.; Uppsala, Sweden
Höij, G.; Miss, Härnösand, Sweden
Holgersen, H.; Stavanger, Norway

*Homoki Nagy, I.; Budapest, Hungary
Hörstadius, S.; Prof., Uppsala, Sweden
Hüe, F.; Pézénas, France
Hurcomb, C.; Lord, London, England
Huxley, J.; Dr., London, England
Hylbom, R.; Stockholm, Sweden
Ingram, C.; Benenden, England
Jacobs, J.; Antwerp, Belgium
Jacobsson, T.; Malmö, Sweden
James, C.; Miss, Barnt Green, England
(Jansson, I.; Miss, Linköping, Sweden)
Jespersen, P.; Dr., Charlottenlund, Denmark
Jespersen, P.; Mrs., Charlottenlund, Denmark
Johansen, H.; Prof., Holte, Denmark
Johnson, H.; Byfleet, England
Jonsson, E.; Stockholm, Sweden
v. Jordans, A.; Dr., Bonn, Germany
Jörgensen, H.; Miss, Copenhagen, Denmark
Jouanin, C.; Paris, France
Jouanin, C.; Mrs., Paris, France
Junge, G. C. A.; Dr., Leiden, Holland
Kalela, O.; Dr., Helsinki, Finland
Karvik, N.-G.; Lidköping, Sweden
*Kelly, J.; Mrs., Alameda, Calif., U.S.A.
Kinnear, Sir Norman; London, England
Klausen, P.; Miss, Copenhagen, Denmark
Kleinschmidt, A.; Dr., Braunschweig, Germany
Knecht, S.; Dr., Freiburg, Germany
Koehler, O.; Prof., Freiburg, Germany
v. Koersveld, E.; Dr., Utrecht, Holland
Kramer, G.; Dr., Wilhelmshaven, Germany
Kramer, G.; Mrs., Wilhelmshaven, Germany
Kreuger, E.; Helsinki, Finland
Krüger, C.; Copenhagen, Denmark
Kuhk, R.; Dr., Möggingen ü. Radolfzell, Germany
Lack, D.; Dr., Oxford, England
Lack, D.; Mrs., Oxford, England
Lagerlöf, S.; Skellefteå, Sweden
Lampio, T.; Helsinki, Finland
Lang, E.; Dr., Basel, Switzerland
Laubmann, A.; Prof., München, Germany
Lauridsen, S.; Copenhagen, Denmark
*Ledent, G.; Liège, Belgium
Lepiksaar, J.; Göteborg, Sweden (formerly in Estonia)
Lepiksaar, J.; Mrs., Göteborg, Sweden (formerly in Estonia)
v. Liechtenstein, H.; Prince, Vaduz, Liechtenstein
Lincoln, F. C.; Washington, D. C., U. S. A.
Lincoln, F. C.; Mrs., Washington, D.C., U. S. A.
Linnman, N.; Stockholm, Sweden
Lloyd, H.; Ottawa, Ont., Canada
Lloyd, H.; Mrs., Ottawa, Ont., Canada
Logan-Home, W.; Edrom, England
Logan-Home, W.; Mrs., Edrom, England
Lohammar, G.; Dr., Uppsala, Sweden
Longfield, C.; Miss, London, England
Løppenthin, B.; Skovlunde, Denmark
Lund, H. Munthe-Kaas; Oslo, Norway
Lundh, E.; Mrs., Norrköping, Sweden
Lundevall, C. F.; Norrköping, Sweden
Lundin, H.; Stockholm, Sweden
Maaldrink, E.; Wierden, Holland
Mackie, A.; Miss, Belfast, N. Ireland
Makatsch, W.; Dr., Bautzen, Germany
Malcolmson, H.; Belfast, N. Ireland
Malmberg, T.; Lund, Sweden
Malmberg, T.; Mrs., Lund, Sweden
van Marle, J.; Amsterdam, Holland
van Marle, J.; Mrs., Amsterdam, Holland
Masch, L.-W.; Dr., Hamburg, Germany
Masch, L.-W.; Mrs., Hamburg, Germany
Maxse, V.; Miss, Pulborough, England
*Mayr, E.; Dr., New York, U. S. A.
Mazelle, E.; Vienna, Austria
Meinertzhagen, R.; London, England
Meise, W.; Dr., Berlin, Germany
Merikallio, E.; Dr., Kerava, Finland
*Merikallio, E.; Mrs., Kerava, Finland
Mills, J.; Dr., Seaford, England

Mills, J.; Mrs., Seaford, England
Moll, R.; Stockholm, Sweden
*Moore, W.; Pymble, Australia
Moreau, R. E.; Berrick near Benson, England
Moreau, R. E.; Mrs., Berrick near Benson, England
*Mountfort, G.; Farnham Common, England
Munck, F.; Mrs., Borgå, Finland
Murphy, R. C.; Dr., New York, U. S. A.
Murphy, R. C.; Mrs., New York, U. S. A.
Naumburg, W.; New York, U. S. A.
Naumburg, W.; Mrs., New York, U. S. A.
Nicholson, E.; London, England
Nöhring, R.; Hamburg, Germany
Nöhring, R.; Mrs., Hamburg, Germany
Noll, H.; Dr., Basel, Switzerland
Noll, H.; Mrs., Basel, Switzerland
Noréhn, N.; Malmö, Sweden
Nyhlén, G.; Stockholm, Sweden
Ogilvie, C.; Dr., Lymm, England
Olivier, G.; Elbeuf, France
Olivier, G.; Mrs., Elbeuf, France
Olrog, C.; Tucumán, Argentina
Olsson, V.; Färgelanda, Sweden
(Olufsen, P.; Copenhagen, Denmark)
(Olufsen, P.; Mrs., Copenhagen, Denmark)
van Oordt, G. J.; Prof., Utrecht, Holland
Österlöf, S.; Näsby Park, Sweden
Otterlind, G.; Fiskebäckskil, Sweden
Otterlind, G.; Mrs., Fiskebäckskil, Sweden
Palm, B.; Vanløse, Denmark
Paludan, K.; Copenhagen, Denmark
Parsons, A.; Redruth, England
Payton, H.; Harrow, England
Peall, O.; Marlborough, England
Peall, O.; Mrs., Marlborough, England
Pearse, T.; Comox, B. C., Canada
Pearse, T.; Mrs., Comox, B. C., Canada
Peitzmeier, J.; Prof., Warburg, Germany
(Persson, S.; Malmö, Sweden)
Petersen, B.; Dr., Uppsala, Sweden
Peterson, R. T.; Glen Echo, Md, U.S.A.
Peterson, R. T.; Mrs., Glen Echo, Md, U. S. A.
Phelps, W. H.; Dr., Caracas, Venezuela
Phelps, W. H.; Mrs., Caracas, Venezuela
Phelps, W. H. Jr.; Caracas, Venezuela
Phelps ,W. H.; Mrs. Jr., Caracas, Venezuela
Pough, R.; Dr., Pelham, N.Y., U. S. A.
Pough, R.; Mrs., Pelham, N.Y., U. S. A.
Poulsen, H.; Copenhagen, Denmark
Poulsen, C. M.; Silkeborg, Denmark
Price, K.; Miss, Oxford, England
Ramberg, N.; Hälsingborg, Sweden
Ramel, C.; Stockholm, Sweden
Rawcliffe, C.; Holyhead, England
(Reeh, R. H.; Copenhagen, Denmark)
Ripley, S. D.; Dr., New Haven, Conn., U. S. A.
Ripley, S. D.; Mrs., New Haven, Conn., U. S. A.
v. Rokitansky, G.; Dr., Vienna, Austria
Rosenberg, E.; Örebro, Sweden
Rudebeck, G.; Lund, Sweden
Runnerström, B.; Uddevalla, Sweden
Ryberg, O.; Dr., Alnarp, Sweden
Samuelson, G.; Kristinehamn, Sweden
Salomonsen, F.; Dr., Copenhagen, Denmark
Sarasin, D.; Basel, Switzerland
Sargent, L.; St. Peter-in-Thanet, England
Sargent, L.; Mrs., St. Peter-in-Thanet, England
Sassi, M.; Dr., Vienna, Austria
*Scheidegger, S.; Dr., Basel, Switzerland
Schifferli, A.; Dr., Sempach, Switzerland
(Schulz, H.; Hamburg, Germany)
Schuster, L.; Frischborn ü. Lauterbach, Germany
Schüz, E.; Dr., Ludwigsburg, Germany
Scott, P.; Slimbridge, England

Sergeant, D.; Cambridge, England
(Serlachius, R.; Helsinki, Finland)
Sibson, R.; Auckland, New Zealand
Sibson, R.; Mrs., Auckland, New Zealand
Skousès, G.; Rome, Greece
Smith, H.; Dr., London, England
Snow, W.; Oxford, England
Spärck, R.; Prof., Copenhagen, Denmark
Stanford, J.; Great Durnford, England
Stanford, J.; Mrs., Great Durnford, England
Steinbacher, J.; Dr., Frankfurt a. M., Germany
Steiniger, F.; Dr., Flensburg, Germany
Stochholm-Dyhrberg, A.; Uppsala, Sweden
Stoffel, J.; Deventer, Holland
Stresemann, E.; Prof., Berlin, Germany
Stresemann, E.; Mrs., Berlin, Germany
Sutter, E.; Dr., Basel, Switzerland
Svane, O. B.; Charlottenlund, Denmark
(Svennilson, E.; Lund, Sweden)
Svärdson, G.; Dr., Traneberg, Sweden
Swanberg, P. O.; Skara, Sweden
Taapken, J.; Leiden, Holland
Täcklind, E.; Mrs., Katrineholm, Sweden
Talbot-Ponsonby, P.; Miss, Slimbridge, England
Tekke, M. J.; 's Gravenhage, Holland
Thibout, G.; Dr., Paris, France
Thibout, G.; Mrs., Paris, France
Thibout, G.; Miss, Paris, France
Thibout, P.; Mrs., Paris, France
Thomasson, K.; Uppsala, Sweden (formerly in Estonia)
Thomson, A. Landsborough; Dr., London, England
Thomson, A. Landsborough; Mrs., London, England
Thulin, S.; Uppsala, Sweden
(Thulin, U.-B.; Stockholm, Sweden)

Tiedemann, M.; Dr., Celle/Hannover, Germany
Tiedemann, M.; Mrs., Celle/Hannover, Germany
Tillisch, C.; Copenhagen, Denmark
Tinbergen, N.; Prof., Oxford, England
Tobiesen, E.; Charlottenlund, Denmark
Tobiesen, E.; Mrs., Charlottenlund, Denmark
Todd, W. E. Clyde; Pittsburgh, Pa., U. S. A.
Toschi, A.; Prof., Bologna, Italy
v. Transehe, N.; Dr., Walsrode, Germany (formerly in Latvia)
Tucker, C.; New York, U. S. A.
Tucker, C.; Mrs., New York, U. S. A.
Turtle, L.; Belfast, N. Ireland
Tutt, H.; Hadleigh, England
v. Udvardy, M.; Dr., Uppsala, Sweden
Ulfstrand, S.; Malmö, Sweden
Välikangas, I.; Prof., Helsinki, Finland
Van Beneden, A.; Liège, Belgium
Van den bergh, W.; Antwerp, Belgium
Van Tyne, J.; Ann Arbor, Mich., U. S. A.
Vaurie, C.; Dr., New York, U. S. A.
Vaurie, C.; Mrs., New York, U. S. A.
Verheyen, R.; Dr., Brussels, Belgium
*Vermeulen, H.; Amsterdam, Holland
*Vermeulen, H.; Mrs., Amsterdam, Holland
Vestergren, G.; Miss, Stockholm, Sweden
v. Vietinghoff-Riesch, A.; Prof., Steinkrug, Germany
Vogt, W.; Washington, D. C., U. S. A.
Vogt, W.; Mrs., Washington, D. C., U. S. A.
Voous, K.; Dr., Amsterdam, Holland
Voous, K.; Mrs., Amsterdam, Holland
(de Vries, G. A.; Baarn, Holland)
Watt, G.; Miss, Newcastle upon Tyne, England
Wells, C.; Torquay, England
Wells, C.; Mrs., Torquay, England

Welti, E.; Mrs., Chêne-Bougeries, Genève, Switzerland
Wendnagel, W.; Basel, Switzerland
Werth, I.; Miss, Leeds, England
Westerskov, K.; Kalø Pr. Rønde, Denmark
Wetmore, A.; Dr., Washington, U.S.A.
Wibeck, E.; Ålsten, Sweden
(Wide, E.; Stockholm, Sweden)
Wigman, A. B.; Hoenderloo, Holland
Wild, A.; Miss, Leuk Stadt, Switzerland
Williams, I. A.; Kew Gardens, England
Williams, I. A.; Mrs., Kew Gardens, England
Wingstrand, I.; Miss, Lund, Sweden
Wingstrand, K. G.; Lund, Sweden
Wingstrand, K. G.; Mrs., Lund, Sweden
Yapp, W.; Birmingham, England
Zastrov, M.; Bromma, Sweden (formerly in Estonia)
Zetterberg, H.; Uppsala, Sweden

# Presidential Address
# Recent Additions to our Knowledge of Prehistoric Birds
## 1933—1949

*Alexander Wetmore*

*Smithsonian Institution, Washington*

The historical record of the Class Aves in fossil deposits is one of the most interesting chapters of our study, though one that is fragmentary and imperfect compared with that of the other warm-blooded group of vertebrates, the mammals. Bones of most kinds of birds are fragile so that they are easily destroyed, and there are in the skeleton no strongly made structures like the teeth of mammals that easily become fossilized, which at the same time offer clear-cut diagnostic characters. Our reliance in the identification of extinct birds is placed mainly on single bones, often on fragments, with only occasional specimens that show several parts of the skeleton of a single individual.

In spite of this handicap in scarcity of material this branch of our science recently has shown many advances, though workers in fossil birds have never been numerous. In 1933, the late Kálmán Lambrecht, fellow member of the International Ornithological Congress, in his Handbuch der Palaeornithologie[1] brought together all information available to that date on this intriguing subject. This volume, of more than one thousand pages, marks one of the greatest contributions in its field, and will remain for years as a standard reference work. It is my proposal now to review the record since Lambrecht's publication through the period from 1933 to the end of 1949, and to offer other comments on the subject, thus projecting the five year review prepared by my fellow worker Dr. Hildegarde Howard in 1938 for the Fortschritte der Paläontologie.

Lambrecht recorded 691 species of fossil birds described from the entire world to December, 1932. In the years that have passed since that date 9 of these species have been eliminated as synonyms, or as based on remains of mammals. During the same time 104 additional species have been described, so that the list at the present moment includes 786 forms. The period from 1932 to 1940 was especially prolific, having been one of the most active in the entire history of the subject.

---

[1] Lambrecht, Kálmán, Handbuch der Palaeornithologie. Berlin, 1933, pp. i–xx, 1–1024, 209 figs.

The geologic distribution of the additional forms is as follows:

| | |
|---|---|
| Cretaceous | 1 |
| Eocene | 11 |
| Oligocene | 14 |
| Miocene | 21 |
| Pliocene | 26 |
| Pleistocene | 24 |
| Recent (prehistoric) | 7 |
| Total | 104 |

It will be observed that the greatest addition has come in the Tertiary where 73 new species have become known, with only 31 in the Quaternary. In the latter, however, great advance has been made in the identification of bones of scores of living species in Ice Age deposits, some from areas where they have not been recorded in modern times. The list of 104 extinct species includes 9 groups so distinct from those now living that they are placed in separate families from any heretofore known. There are several others that are rated as subfamilies, and many previously unknown genera.

The geographic distribution of the new finds has been broad, with Australia as the only prominent gap in our knowledge of the subject. The 19 new species recorded from Europe come from France, Switzerland, Germany (3), Ukraine (7) and Azerbaijan (7). In Asia 4 localities gave 5 species, two from Kazakh, one from another point in southwestern Siberia, one from Iran, and two from Inner Mongolia. Other occurrences include Tanganyika, Java, New Zealand (3) and the island of Hawaii. There are 2 from Ecuador and 3 from Argentina in South America, 5 from Mexico, 4 from the West Indies, and one from Alberta, Canada. The remaining 58 are reported from the United States, where 12 states covering the entire breadth of the country are included. California with 16 additional species has been the most prolific, followed by South Dakota with 14, and Wyoming and Nebraska each with 7.

The oldest of these additional finds is from the Belly River series of the Upper Cretaceous in Alberta, Canada, described by R. M. Sternberg as *Caenagnathus collinsi*, placed in a distinct family, the Caenagnathidae, and in a separate order, the Caenagnathiformes. This is named from a single bone, a complete mandible measuring 220 mm in length, in which outstanding characters are the lack of teeth, the smooth, completely fused symphysis of the dentaries, and the cancellous form where the bone is not reduced to thin sheets. Other species of Cretaceous birds in which the jaws are known possessed teeth, so that the present individual is an anomaly in this respect. The head seems to have been rather slender, being about one fourth longer than that of the largest living swans (a comparison that relates to size alone, and that is no indication whatever of relationship). Beyond this there is little that may be said relative to the form or type of the creature that bore this jaw. It must be pointed out, however, that while described as a bird, with characters that seem to fit it in that class, there is strong possibility that *Caenagnathus* may prove to be an unusual type of the reptilian group of dinosaurs whose remains are so characteristic of the Cretaceous deposits in the area of Canada in which the type was found. The fused symphysis, the large mandibular foramen and lack of teeth point to avian status, but, it must be added, there is nothing in these that can not be duplicated in Reptilia. In the conformation of the articular surface, and in the upward curvature and general form at the symphysis there is strong reptilian suggestion. In the present acceptance of *Caenagnathus* as a bird it is placed provisionally near the ostriches, rheas, cassowaries, moas, elephant-birds, kiwis and tinamous, a position that is wholly tentative, and that has been decided on the basis of antiquity rather than on supposed close relationship to any of these groups.

The entire Cretaceous record of the Class Aves is so small that it must be recognized as fragmentary to a high degree. Two groups of toothed birds, the Hesperornithiformes, with 5 known species, diverlike in form, characterized by teeth in grooves, and the Ichthyornithiformes with 10 kinds now recognized marked by well developed wings and the teeth in distinct and separate sockets, all from North America, are the most completely known. Aside from these, six species found in European localities include an ancestral gooselike bird, *Gallornis straeleni*, so fragmentary that its supposed anatine relationship may be questioned, two divers *Enaliornis barretti* and *E. sedgwicki*, two primitive flamingos, *Scaniornis lundgreni* and *Parascaniornis stensiöi*, and finally *Elopteryx nopcsai*, related to the cormorants. The primitive beginnings of our living birds in Mesozoic time remain obscure.

The 11 additional species now added to the record of the remote time of the Eocene, with their many millions of years of antiquity, have produced new and intriguing information regarding early stages in some of our existing birds. It is in the Eocene that we find our main knowledge of the early record of our living orders of the avian class. As more information becomes available it appears that many, if not most, of the fossils of this period are set apart by such definite characters that they mark peculiar families or subfamilies, now extinct. Several additional groups in this category have now been added to our list.

A small duck, *Eonessa anaticola* Wetmore, from the Upper Eocene of Utah, in the United States, is about the size of the living lesser scaup duck (*Aythya affinis*), but has more slender bones in the wing, being more like the small diving ducks of the genus *Oxyura*, whose species are widely distributed. The fossil is separated in a distinct subfamily Eonessinae.

One of the most completely known of the additional Eocene forms is *Neocathartes grallator* (Wetmore), placed in a distinct family Neocathartidae and a separate superfamily Neocathartoidea in the suborder of American vultures the Cathartae. Most of the skeleton, including the skull, was found by Dr. John Clark, of the Carnegie Museum, in the Upper Eocene of Wyoming, with many of the most delicate structures preserved, even part of the bones supporting the tongue being present. This is one of the most curious of the fossil species that it has been my fortune to describe. The wings were degenerate, though still functional for flight, while the legs were greatly elongated so that the bird was evidently terrestrial. From the texture of the surface of the cranium, and the relative size of the irregular furrows for blood vessels running out from the margin of the orbit, it is believed that the head was covered with a thickened skin bare of feathers like that of modern Cathartae. The strong cervical vertebrae indicate a thickened muscular neck. While the sternum is not preserved the weakened wing and coracoid give support to the supposition of slight development of the breast muscles and their corresponding attachments. We have the anomalous picture, therefore, of a terrestrial vulture that walked or ran, flying only short distances, perhaps only at intervals; in other words a species that in general form presents in the suborder Cathartae an appearance among its kindred similar to that offered by the living secretary-bird, (*Sagittarius serpentarius*) in the suborder Falcones, containing the other groups of the order Accipitriformes.

Parts of the leg bones of a crane-like bird from the Lower Eocene of Wyoming, *Geranoides jepseni* Wetmore, represent a bird with long, slender legs about the size of the living little brown crane (*Grus canadensis canadensis*). The wide separation of the articular supports for the toes is highly peculiar, and is one of the principal reasons for placing this bird in a separate family the Geranoididae.

Another new family, the Eogruidae, placed in the superfamily Gruoidea, has been erected for the peculiar *Eogrus aeola* Wetmore, from the Upper Eocene of Inner Mongolia. The specimens known include a number of tarsometatarsi and tibio-tarsi that, while crane-like, present characters in the reduction of the size of the trochlea and of the support of the lateral toes, with corresponding increase in the middle trochlea, that indicate that it was specialized for running, in this suggesting the related cariama (*Cariama cristata*) of South America, but being even more developed for coursing. The form of the trochlea, in fact, presents an interesting duplication of the development found in the rhea (*Rhea americana*), far removed from *Eogrus* in a systematic sense. The assumption is that it was crane-like in general form, but, from one fragment of the wing found associated with the leg bones, a bird of somewhat weakened flight.

In the Order Gruiformes there is also *Telecrex grangeri* Wetmore from the Upper Eocene of Inner Mongolia in a separate subfamily, the Telecrecinae, marked by the peculiar compression and flattening of the head of the humerus. The bird seemingly had habits similar to such living genera as *Rallus* and *Aramides* of the subfamily Rallinae, and may be considered ancestral to these. At the same time *Telecrex* seems more remotely connected with the more aquatic, swimming forms of the family.

Another of the strange groups of the Eocene is the family Protostrigidae, described by the author, in which we now have 4 species of primitive owls based on fragmentary specimens. These seem more nearly related to the typical owls, the Strigidae, than to the barn owls, the Tytonidae, in the form of leg and wing bones.

Another of the interesting birds of this early period in the Tertiary is the ostrichlike form *Eleutherornis helveticus* Schaub from Switzerland, described from a fairly well preserved pelvis. This offers some peculiarities but seems to belong in an ancestral group that has produced the living ostriches, though it should be separated from them as a distinct family, the *Eleutherornithidae*. It represents a most important early step in the history of the Struthioniformes, since it extends the known range of the order geographically from southern Russia and Greece to western Europe, and geologically from the lower Pliocene to the Eocene. Its greatest importance is found in its indication of affinities with the carinate groups, while being at the same time of unquestioned ratite stock. It is thus a link that decides the long debate on the ancestry of the struthious birds, since it indicates clearly that these flightless groups of modern times have come from flying ancestors, and not, as some have contended, from a distinct line in which the individuals have always been flightless.

While the giant running birds of the Eocene known as diatrymas, placed in our classification near the crane-like birds, have been described primarily from North America, one species referred questionably to the genus *Dia-*

*tryma* was named from Switzerland by Schaub in 1929. Lambrecht was convinced of the allocation in this genus, but Dr. Schaub has preferred to consider the relationship tentative. Gaillard now has described another species from the Eocene of France as *Diatryma ? cotei*. Here again it seems probable that a distinct family group is indicated for the two European forms, though further study of the material is required to determine this.

A true hornbill (family Bucerotidae), named *Geiseloceros robustus* by Lambrecht, from the Eocene of Germany, is a highly important record, both for its locality in central Europe, and as a point in the history of this curious family of birds. There have been only two other fossils, *Cryptornis antiquus* (Gervais) and *Homalopus picoides* Milne-Edwards, attributed to this group, both being assigned here with an uncertainty that from present knowledge seems quite warranted.

To continue the roster of additional families, from the Oligocene of Mendoza, Argentina, Rusconi has described *Cunampaia simplex*, marked by reduction in the carpal portion of the wing, placing it in a separate family Cunampaiidae in the Suborder Phororhaci. It is said to be quite different from *Phorarhocos*, but is considered to have been of similar terrestrial habit.

Of the 13 other species now reported from the Oligocene four are hawks. Three of these are of the broad-winged, soaring type, called buzzards where English is spoken in the Old World, all from the Great Plains section of the United States, and all placed at present in the genus *Buteo*. One of these is represented by a skull in fair state of preservation, an unusual circumstance since most of our knowledge of fossils in this group has come from fossilized limb bones. Except for larger size, this species, *Buteo grangeri* Wetmore and Case, is quite similar to the living red-tailed hawk (*Buteo jamaicensis*), differing only in the minor details of contour and outline that distinguish species. There is thus indication of great antiquity for this style of predator, which has continued for millions of years without radical change to the present day. *Buteo antecursor* Wetmore from the Upper Oligocene of Wyoming, slightly larger than the largest living rough-legged hawks is another indication of the early appearance of the slow-flying, rather sluggish hawks that have developed throughout the World in so many diverse, yet closely allied forms. Another, even larger, species in this group from a slightly older stage (Oreodon beds) in the Oligocene of Colorado is *Buteo fluviaticus* A. H. Miller and C. G. Sibley. Finally there is *Palaeoplancus sternbergi* Wetmore, from Upper Oreodon beds in the Oligocene of Niobrara County, Wyoming, a bird about the size of a golden eagle (*Aquila chrysaëtos*), with moderate wings, strong legs and feet, and relatively weakly developed tail, that may have been less adapted to soaring or to rapid flight than most of our modern hawks. The peculiarities of this species are such that it is placed in the separate subfamily Palaeoplancinae in the Accipitridae, between the Buteoninae and the Circaëtinae. There is hint that even greater and more powerful eagles lived during the Upper Oligocene, as I have examined a talon from the Torrington deposits of Wyoming that indicates a foot as strong as that of the largest and fiercest known among living species in the family, being fully equal to that of *Pithecophaga*, the modern monkey-eating eagle of the Philippines.

Tugarinov, in describing *Agnopterus turgaiensis*, from the Turgai region in the Kazakh S. S. R., has added a third species to the ancestral flamingo-like birds in the family Agnopteridae.

Of two additional members of the Aramidae, the limpkins or crying birds, allied to the cranes, *Badistornis aramus* Wetmore from the White River Oligocene of South Dakota appears directly ancestral to the living member of the family, *Aramus guarauna*, being a link that leads toward the family of true cranes. The second species *Gnotornis aramiellus* Wetmore, also from White River deposits in South Dakota, while a true limpkin is notable for being only about one third the size of the other known species of the family, both living and fossil. This is another interesting case where there are two size levels, one large and one small, in groups of related species that, except for dimension, are quite similar. *Bathornis geographicus* Wetmore from South Dakota is the fourth species now known in the peculiar family Bathornithidae of Oligocene times, allied to the living cariamas.

The great running birds with huge heads of southern South America, best known through the forms of the genus *Phororhacos*, are among the strangest of the fossil birds of the new world. *Andrewsornis abbotti* Patterson, from near the middle of the Oligocene, marks an additional form, described from a skull, coracoid and a few bones of the feet from the Deseado formation of the Territory of Chubut in Patagonia, being the first species of its family from this particular formation. In his discussion of its relationships, which place it in the family Phororhacidae, Patterson recognizes another family, the Psilopteridae, for *Psilopterus* and its allies, which, with the Brontornithidae, makes three family groups in the suborder Phororhaci. The mandible in *Andrewsornis* measures 394 mm in length, an indication of the great size of the head in this tremendous bird. A supposed Albatross, *Manu antiquus* Marples, has been named from Upper Oligocene deposits in New Zealand.

In the Miocene period the most of the fossil birds are more nearly like those of the present day, though strange groups that have become extinct in geologic time are found. The 20 additional species added to our list since Lambrecht's work offer much of interest in increase of our knowledge. All have been described from the United States of America.

Two additional species of boobies, *Sula stocktoni* L. H. Miller and *Sula avita* Wetmore, increase the American fossil forms now known in this group to 10, of which 9 have been described from the Miocene, an interesting fact when we recall that the living species in the family Sulidae also number 9. Evidently these birds have long been abundant over the seas, particularly along American shores.

A flamingo, *Megapalaeolodus connectens* A. H. Miller, from the lower Miocene of South Dakota is the first record of this interesting family in Tertiary deposits in the New World, though in Europe the group is abundant in deposits of the late Oligocene in France. The American bird seems related to the Old World *Palaeolodus*, these two genera being somewhat less specialized in form than the living species of the family.

From these same lower Miocene beds in South Dakota comes *Paranyroca magna* A. H. Miller and L. V. Compton, type of a distinct family, the Paranyrocidae, in the Anseriformes, a bird with the size of a swan but highly specialized for swimming and diving in a manner analogus to the diving ducks. In the same deposits Dr. Miller has also found *Dendrochen robusta* of the subfamily of tree-ducks, the Dendrocygninae, which previously has not been known back of the Upper Pliocene. *Dendrochen* has some characters in the humerus that suggests an original connection between the two subfamilies of the tree-ducks and the geese.

The five hawklike birds added to the Miocene list are a further indication of the great abundance of this group in the latter part of the Tertiary. *Falco ramenta* Wetmore is the earliest record of the true falcons, since the supposed *Falco falconellus*, named by Shufeldt from the Eocene, proves to be a composite of fragments of several species of birds, none of which can be identified to family, or even to order, so that this species must be relegated to the limbo of forms that have been named on such insufficient ground that they may not be placed in our scheme of classification. *Falco ramenta* was a pygmy species, related to the pigeon hawks or merlins, but smaller than the living kinds.

*Palaeoborus howardae* Wetmore and *P. rosatus* A. H. Miller add two further species to the forms of the subfamily Aegypiinae, which seem to have been common in the New World up into Pleistocene times, but since then to have disappeared. Another large hawk, somewhat larger than the ferruginous roughleg (*Buteo regalis*) of the ordinary, broad-winged group, *Miohierax stocki* Howard from the Lower Miocene of California, is marked by peculiarities of the foot, which seems unusually strong. Still another in this assemblage, *Palaeastur atavus* Wetmore, also from the Lower Miocene, shows affinities with *Spizastur, Spizaëtus* and *Leucopternis,* all of them American genera.

Our knowledge of the Cracidae, a family of gallinaceous birds, peculiar to the Americas, that are in large part arboreal in habit, is increased by two additional species, *Ortalis tantala* Wetmore and *Ortalis pollicaris* A. H. Miller. The first named is the smallest known member of the family, being less than one-half the size of the living species of the genus. While placed now in *Ortalis* it is probable that it represents an extinct genus, a point that may not be decided at present since modern skeletons of part of the species of the family are not yet available for examination. *Ortalis pollicaris,* also from the lower Miocene, is similar in size to the living species, so at that time there were two sizes among these birds, one being very much smaller than the other. While these two were related to the living kinds, they both probably will be separated generically at some future date. Though there has been a species, *Ortalis phengites* Wetmore, known for some time from the Pliocene, these two additional extend the known time range for these birds to a much older period.

Among the three other additional gallinaceous birds there are two quail, *Miortyx teres* A. H. Miller, from the lower Miocene of South Dakota, unlike living genera, and *Cyrtonyx cooki* Wetmore, from the Upper Miocene of Nebraska, that is similar to the living species of this genus but is about one-fourth larger. *Tympanuchus stirtoni* A. H. Miller is a prairie chicken closely allied to the two living species of this group.

From the Miocene of Florida there has come *Rhegminornis calobates* Wetmore, sole species of the family Rhegminornithidae, a shore-bird, as large as a medium-sized curlew, related to the plovers and snipe, but also showing some approach to the jaçanas. From the form of the foot the suggestion is that it may have walked over floating vegetation. A guillemot *Miocepphus mcclungi* Wetmore, from Maryland, and a small owl *Strix dakota* A. H. Miller from South Dakota, complete the roster of the additions to the Miocene. The owl is peculiar for being the smallest of known forms in its genus.

In the 27 additional species reported from the Pliocene the additional data comes largely from the 17 described from the United States. These include 2 loons, 2 shearwaters, a cormorant, a flamingo, a goose, a teal, a quail, a crane, a rail, and a murrelet, that are placed in living genera, and may be passed over here without further comment, except to note that they mark important points in the history of their respective groups.

The gannet genus *Miosula,* known previously from a species in the Miocene marked by small wings and large legs, is now extended into the Pliocene by *Miosula recentior* Howard. This younger form shows even greater development of the legs and corresponding decrease in the wings, thus paralleling a similar circumstance among the cormorants. As Dr. Howard remarks, *Miosula* seems to have disappeared on achieving the stage shown in the living flightless cormorant *Nannopterum harrisi* of the Galápagos Islands. In the group of Aegypiine vultures, in modern times restricted to the Old World, two additional species have been found, viz., *Neophrontops dakotensis* Compton and *N. venustus* Wetmore, both from South Dakota.

The auk family is represented by a large puffin *Pliolunda diegense* L. H. Miller. Tugarinov has described a new falcon of small size, from near Pavlodar in the Kazakh S. S. R., as *Sushkinia pliocaenica*, which he compares to the group of African kestrels of the subgenus *Dissodectes* in the genus *Falco*. The giant species from the Province of Buenos Aires, Argentina, *Mesembriornis rapax* (Kraglievitch), in the family Phororhacidae, had the skull 440 mm in length, with a strongly hooked beak. *Urmiornis abeli* was named by Lambrecht on the basis of three fossil footprints from Iran which he considered to be those of a crane. While he placed this as a distinct species allied to the Lower Pliocene crane called *Urmiornis maraghanus* by Mecquenem, in 1925, from Maragha, Iran, this allocation must be considered tentative because of the difficulty in aligning tracks left by a living bird and fossil bones, so that it seems best to locate this occurrence in the limbo of incertae sedis.

Of eight new forms named by Serebrovsky and Tugarinov seven come from near Odessa in the Ukrainian S. S. R., marking a considerable addition from that part of Europe. *Pliocarbo longipes* Tugarinov, while related to modern cormorants, had the metatarsus much more slender, indicating an aquatic species, but one less specialized for swimming than its living relatives. *Alectoris pliocaenica* and *Ammoperdix ponticus* are closely similar to living birds in these genera. *Pliogallus coturnoides* Tugarinov was like the modern quail, *Coturnix*, but had more strongly developed wings. Serebrovsky considers this probably congeneric with *Coturnix*. A bustard, *Chlamydotis pliodeserti* Serebrovsky, is apparently closely related to living forms, while a wader *Totanus numenioides* of the same author was like the Redshank but was decidedly larger. An owl, *Asio pigmaea* Serebrovsky, was similar to the modern short-eared owl but was marked by much smaller size. *Sushkinia pliocaenica* Tugarinov the final species, from southwestern Siberia, has been mentioned in a preceding paragraph.

The 24 new species named from Pleistocene deposits indicate only a part of the picture of additions to the fossil record, since bones of a considerably larger number of living species have been identified in fossil deposits. Especially notable is an extensive list of 57 species from the Kirov deposits at Binagada, near Baku in Azerbaijan.

Further exploration of the Pleistocene areas in Java in which the famous fossil man *Pithecanthropus* was found has brought to light a few bones of birds which have come to the hands of the author for study. They include a humerus of the modern crane *Grus grus,* indication that in the Ice Age this species ranged south into the Greater Soenda Islands, instead of reaching only to northern India and China as at present. If we assume that the crane in Pleistocene times nested and reared its young on northern tundras, the occurrence in this period in Java may be interpreted as indication of migration to a more southern locality after the breeding season. Naturally this is purely speculative since a related crane, *Grus canadensis* of North America, while migrant in part of its population, has resident forms in the south in Florida, Cuba and the Isle of Pines.

A more intriguing find in these Javan deposits is a great stork, *Leptoptilos titan* Wetmore, known from a complete metatarsal bone. From comparisons made with the largest of living storks it is evident that the Javan species may have stood six feet or more in height.

*Stercorarius shufeldti* Howard from the Pleistocene deposits at Fossil Lake, Oregon, where remains of hundreds of birds have been found, is the first fossil representative of the family of hunting gulls, the Stercorariidae. While in form a true jaeger (*Stercorarius*) it was as large as the great skua (*Catharacta skua*).

Additions to the order of perching birds include *Pipilo angelensis* Dawson, a large sparrowlike form, and *Pandanaris convexa* A. H. Miller, a member of the New World family Icteridae. Both of these come from the pitch deposits of California that have yielded such abundant remains of birds. Other additions are a pelican, a swan, a goose and two ducks named by Serebrovsky from near Baku, all except the goose being only subspecifically different from the living populations. Dr. Howard has described a carrion hawk, *Polyborus prelutosus,* in which she has separated two subspecific forms, one from California and one from Nuevo León in northern México. She has also distinguished another falcon, *Falco oregonus,* from the Fossil Lake deposits of Oregon. Further species announced by Serebrovsky from Baku include a crane, *Sarcogeranus bogatshevi,* and a ruff, *Philomachus binagadensis.* Spillman has described a duck and a parrot from Ecuador on somewhat uncertain grounds, and Loye Miller a turkey, *Meleagris crassipes,* and a curlewlike shorebird, *Palnumenius victima,* from northern México.

In this survey it is desirable to include mention also of 8 extinct species that are known only from their bones in deposits of the Quaternary, being found in Recent deposits laid down since the close of the Pleistocene.

In New Zealand Archey has published an extensive review of the Moas, flightless birds some of which were in existence when the Polynesians reached those islands. In the course of this review he has described two new species, *Megalapteryx benhami* and *Pachyornis mappeni*. His work includes accounts of eggs, skin, feathers, and tracheal rings of these birds, which he believes were exterminated by the earliest men to reach New Zealand, so that they had disappeared before the ancestors of the present Maori tribes arrived in 1350 A. D. Recently other extensive finds of the bones of these curious birds have been made.

From what is known as the Pahala formation on the island of Hawaii Wetmore has named *Geochen rhuax*, a relative of the living Cape Barren goose *Cereopsis novaehollandiae* of southern Australia. As *Geochen* has no close relationship with the nene, *Nesochen sandvicensis*, now living in Hawaii, it introduces a completely new and unexpected element in the avifauna of that oceanic group.

Cavern deposits on Great Exuma Island in the Bahama Islands, West Indies, have given two predatory birds of huge size, that supposedly lived on the large rodent *Geocapromys*, also extinct, whose bones are found abundantly with those of the birds. The first, *Titanohierax gloveralleni* Wetmore, was an eagle related to the long-legged *Hypomorphnus*, common today in tropical America. The second, an equally large owl, *Tyto pollens* Wetmore, is allied to *Tyto ostologa* Wetmore named from bones found in caverns in Haiti. Apparently, large species of the Tytonidae, which I consider a well-defined family, were dominant in prehistoric times in the West Indies, as I have evidence, as yet undescribed, of an even larger kind on the island of Cuba.

In connection with problems in classification Dr. Hildegarde Howard has made an interesting application of Dr. George Gaylord Simpson's suggestion that overlapping forms of two geological periods should be considered a chronocline, with the connection between the two indicated by the same specific name, with an added, distinctive term to make a trinomial. In work on the many Pleistocene species in the Fossil Lake avifauna in eastern Oregon Dr. Howard has listed the large extinct grebe of these deposits as *Aechmophorus occidentalis lucasi*, thus placing it as a direct ancestor of the modern western grebe *Aechmophorus occidentalis*, which is abundant today in the same region. Also, she has cited the coot of the Pleistocene in that area as *Fulica americana minor*, as a close ancestor of the living American coot *Fulica americana*. This seems a reasonable procedure, and one that represents the facts, though in check-lists that include both modern and fossil species it may be necessary to include footnotes that explain the time element involved, to avoid confusion in the understanding of distribution of the races of these birds.

The very considerable increase in our knowledge of fossil birds that has been gained in the past 17 years has served to support the idea that I have long held relative to the evolution of the living species of our modern world. I report here again my firm belief that birds as a class had their maximum abundance in Tertiary ages, and that our living kinds had their evolution both as genera and as species in the Miocene and Pliocene periods. The space of Quaternary time that followed has been one of rigor, pressure and extermination, beginning with the Pleistocene, when sheets of ice covered large areas in the Northern Hemisphere where formerly birds had found congenial environments for increase and diversification, and culminating in our present age when Man as the dominant creature has overrun the Earth, converting it to his own uses, not only destroying by hand many of the birds and other creatures that formerly flourished, but also usurping and changing the land so that great numbers of birds have been destroyed because of loss of their proper habitats.

The former abundance of birds during Miocene and Pliocene times over wide areas in what are now temperate regions may be surmised when we become familiar with present day quantity and variety in the richest of tropical areas. We have hints in the preservation of fragments of the larger birds of these Tertiary times of the variety that existed, but the number of species of smaller kinds is only surmise. Abundant fragments of small birds of peculiar form in such deposits as the Rexroad of the Upper Pliocene of Kansas give hints of many unknown species, but mainly in so fragmentary condition that they may not be identified. If Colombia and Venezuela, in northern South America, today have each more than 2000 forms of birds it seems quite certain that an equal number were found, for example, in the central and southern parts of the United States of America at the close of the Tertiary. And equally certain that hundreds and thousands of such species have disappeared.

The period of avian evolution truly has been vast, particularly since modern knowledge has multiplied many fold earlier ideas as to the extent in years of the geologic scale. Such developments as the six foot long tail feathers of Reinhardt's pheasant, or the curious and varied plumes of the birds of paradise, must have required not hundreds but many thousands of years.

I have remarked in another connection that to me each fossil part of a bird, whether broken or complete, represents a tiny window through which we may peer into the avifauna of the past. There, clothed by imagination in flesh and feathers, these broken fragments present an intriguing picture of strange and interesting species. In our modern excursions we note the occurrence of our birds in terms of space, recording both their day by day occurrence in the ecologic environments that they seek, and the location of these environments in the political terms of present day geography. Our work with fossils deals likewise with geographic distribution but to a less confining degree, since it locates the species also in terms of geologic time. Our avian picture thus becomes three-dimensional, with the time element extending into the past far greater than the plane on which our modern records rest.

We may look to more and more information from fossils to broaden our knowledge of the steps in the evolution of our modern birds.

## Appendix

## List of fossil birds described from 1933 to the end of 1949

The references that follow, arranged in systematic order, are those that have been located in a search of the literature for the period following the appearance of Lambrecht's Handbuch der Palaeornithologie in 1933 to December 31, 1949. As descriptions of fossil birds appear in many scattered sources it is probable that some have been overlooked.

Order CAENAGNATHIFORMES.

Family CAENAGNATHIDAE.

*Caenagnathus collinsi* Sternberg, Journ. Pal., vol. 14, no. 1, January, 1940, p. 81. Upper Cretaceous: Pale beds of the Belly River series, Quarry no. 112, 1 1/2 miles due south of the mouth of Sand Creek, Alberta, Canada.

Order STRUTHIONIFORMES.

Family ELEUTHERORNITHIDAE.

*Eleutherornis helveticus* Schaub, Eclog. Geol. Helveticae, vol. 33, no. 2, 1940 (June 6, 1941), p. 283, figs. 1–4. Eocene: Bohnerz formation, near Egerkingen, Switzerland.

Family STRUTHIONIDAE.

*Struthio oldawayi* P. R. Lowe, Ibis, ser. 13, vol. 3, no. 4, October, 1933, p. 654. Lower Pleistocene: Bed no. 1, Oldaway series, Oldaway, Tanganyika Territory.

### Order DINORNITHIFORMES.

#### Family ANOMALOPTERYGIDAE.

*Megalapteryx benhami* Archey, Bull. Auckland Inst. Mus., no. 1, May 29, 1941, p. 35. Recent (prehistoric): Cave deposits in the Mt. Arthur Table-land, Nelson, South Island, New Zealand.

*Pachyornis mappeni* Archey, Bull. Auckland Inst. Mus., no. 1, May 29, 1941, p. 35. Recent (prehistoric): Cave deposits at Mangataoki, North Island, New Zealand.

### Order GAVIIFORMES.

#### Family GAVIIDAE.

*Gavia concinna* Wetmore, Journ. Morph., vol. 66, no. 1, January 2, 1940, p. 25, figs. 1–4. Lower Pliocene: Etchegoin beds, Sweetwater Canyon, 5 $^1/_2$ miles east of King City, Monterey County, California.

*Gavia palaeodytes* Wetmore, Proc. New England Zoöl. Club, vol. 22, June 23, 1943, p. 64, figs. 1–2. Middle Pliocene: Phosphate pits, Pierce, Florida.

### Order PROCELLARIIFORMES.

#### Family DIOMEDEIDAE.

*Manu antiquus* Marples, Trans. Roy. Soc. New Zealand, vol. 76, pt. 2, September, 1946, p. 133, pl. 6, figs. 7–9. Upper Oligocene: Maerewhenua Greensand, Duntroonian age, near Duntroon, North Otago, New Zealand. (Allocation to family not wholly certain.)

#### Family PROCELLARIIDAE.

*Puffinus kanakoffi* Howard, Carnegie Inst. Washington, Publ. 584, June 22, 1949, p. 187, pl. 2, figs. 3, 5. Middle Pliocene: San Diego formation, Los Angeles Museum locality 1080, on Washington Boulevard Freeway, San Diego, California.

*Puffinus felthami* Howard, Carnegie Inst. Washington, Publ. 584, June 22, 1949, p. 194, pl. 2, figs. 4, 6. Lower Pliocene: 3 miles north of Corona del Mar, Orange County, California.

### Order PELECANIFORMES.

#### Family PELECANIDAE.

*Pelecanus crispus palaeocrispus* Serebrovsky, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 33, nos. 7–8, December 20, 1941, p. 472. Pleistocene: Kirov deposits, Binagada, near Baku, Azerbaijan.

*Pelecanus haliaeus* Wetmore, Smithsonian Misc. Coll., vol. 87, no. 20, December 27, 1933, p. 3, figs. 1–2. Upper Pliocene: Hagerman lake beds, about 2 miles west of Hagerman, Idaho.

#### Family SULIDAE.

*Sula stocktoni* L. H. Miller, Publ. Univ. California at Los Angeles, Biol. Sci., vol. 1, no. 5, March 12, 1935, p. 75, fig. 2. Upper Middle Miocene: Temblor phase, Monterey formation, near Lomita, California.

*Sula avita* Wetmore, Proc. U. S. Nat. Mus., vol. 85, January 14, 1938, p. 22, figs. 2–3. Miocene: Calvert formation, on Chesapeake Bay, near Plum Point, Maryland.

*Miosula recentior* Howard, Carnegie Inst. Washington, Publ. 584, June 22, 1949, p. 190, pl. 2, figs. 1–2 a. Middle Pliocene: San Diego formation, Los Angeles Museum locality 1071, Curlew Street, opposite Otsego Drive, San Diego, California.

*Morus reyana* Howard, Condor, vol. 38, no. 5, September 15, 1936, p. 213, fig. 37. Pleistocene: Upper San Pedro formation, near Playa del Rey, California.

### Family Phalacrocoracidae.

*Pliocarbo longipes* Tugarinov, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 26, no. 2, January 20, 1940, p. 197, figs. 1, 2. Lower Pliocene: Pontian limestone, Slobodka, near Odessa, Ukrainian S. S. R.

*Phalacrocorax kennelli* Howard, Carnegie Inst. Washington, Publ. 584, June 22, 1949, p. 188, pl. 3, figs. 7–8 a. Middle Pliocene: San Diego formation, Los Angeles Museum locality 1080, on Washington Boulevard Freeway, San Diego, California.

## Order Ciconiiformes.

### Family Ciconiidae.

*Leptoptilos titan* Wetmore, Journ. Pal., vol. 14, no. 5, September, 1940, p. 447, figs. 1–5. Upper Pleistocene: Watoealang, near the Solo River, central Java.

*Mycteria wetmorei* Howard, Condor, vol. 37, no. 5, September 15, 1935, p. 253, fig. 47. Pleistocene: Rancho La Brea, Los Angeles, California.

### Family Agnopteridae.

*Agnopterus turgaiensis* Tugarinov, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 26, no. 3, January 30, 1940, p. 308, fig. 2. Oligocene: Indricotherium beds, Lake Chelkar-Teniz, Turgai region, Kazakh S. S. R.

### Family Phoenicopteridae.

*Megapalaeolodus connectens* A. H. Miller, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, no. 4, June 22, 1944, p. 86, fig. 1. Lower Miocene: Rosebud beds, late Arikareean, at Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

*Phoenicopterus stocki* L. H. Miller, Wilson Bull., vol. 56, no. 2, June, 1944, p. 77, figs. 1–2. Pliocene: Rincón beds, Chihuahua, México.

## Order anseriformes.

### Family Paranyrocidae.

*Paranyroca magna* A. H. Miller and L. V. Compton, Condor, vol. 41, no. 4, July 15, 1939, p. 153, fig. 34 A, C, D, E. Lower Miocene: Rosebud formation, Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

### Family Anatidae.

*Cygnus olor bergmanni* Serebrovsky, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 33, nos. 7–8, December 20, 1941, p. 472. Pleistocene: Kirov deposits, Binagada, near Baku, Azerbaijan.

*Anser azerbaidzhanicus* Serebrovsky, Compt. Rend. (Doklady) Acad. Sci. U. S. S. R., vol. 27, no. 7, June 10, 1940, p. 766. Pleistocene: Kirov deposits, Binagada, near Baku, Azerbaijan.

*Chen pressa* Wetmore, Smithsonian Misc. Coll., vol. 87, no. 20, December 27, 1933, p. 9, figs. 5 8. Upper Pliocene: Hagerman lake beds, near Hagerman, Idaho.

*Geochen rhuax* Wetmore, Condor, vol. 43, no. 4, July 23, 1943, p. 146, fig. 39. Recent (prehistoric period, possibly several thousand years old): Pahala formation (probably), Mount Kaumaikeohu, above Pahala, Island of Hawaii.

*Dendrochen robusta* A. H. Miller, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, no. 4, June 22, 1944, p. 88, fig. 3. Lower Miocene: Rosebud beds, late Arikareean, Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

*Anas oligocaenica* Tugarinov, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 26, no. 3, January 30, 1940, p. 307, fig. 1. Upper Oligocene: Agyspe, Lake Aral, southwestern Siberia.

*Anas platyrhynchos palaeoboschas* Serebrovsky, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 33, nos. 7–8, December 20, 1941, p. 471. Pleistocene: Kirov deposits, Binagada, near Baku, Azerbaijan.

*Anas integra* (A. H. Miller). *Querquedula integra* A. H. Miller, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, June 22, 1944, p. 90, fig. 4. Lower Miocene: Rosebud beds, late Arikareean formation, Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

*Archaeoquerquedula lambrechti* Spillmann, Proc. Eighth Amer. Sci. Congr., vol. 4, September 3, 1942, p. 387, fig. 9. Pleistocene: Peninsula of Santa Elena, Ecuador.

*Anas bunkeri* (Wetmore). *Nettion bunkeri* Wetmore, Univ. Kansas Sci. Bull., vol. 30, pt. 1, May 15, 1944, p. 92, figs. 1–3. Upper Pliocene: Rexroad fauna, late Blancan age, Meade County, Kansas.

*Aythya marila asphaltica* Serebrovsky, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 33, nos. 7–8, December 20, 1941, p. 471. Pleistocene: Kirov deposits, Binagada, near Baku, Azerbaijan.

*Eonessa anaticula* Wetmore, Journ. Pal., vol. 12, no. 3, May 1938, p. 280, figs. 1–5. Upper Eocene: Uinta C horizon, Myton Pocket, Utah.

### Order FALCONIFORMES.

#### Family NEOCATHARTIDAE.

*Neocathartes grallator* (Wetmore). *Eocathartes grallator* Wetmore, Ann. Carnegie Mus., vol. 30, May 24, 1944, p. 58, pls. 1–5, figs. 1–10. Upper Eocene: Upper Washakie beds, one-half mile north of Dobe Town Road crossing, Sweetwater County, Wyoming.[1]

#### Family CATHARTIDAE.

*Eocathartes robustus* Lambrecht, Nova Acta Leopoldina, vol. 3, no. 14, 1935, p. 362, pl. 1, fig. 2. Middle Eocene: Lutétian beds, Cecilie Mine, Mücheln im Geiseltal, Merseburg, Halle, Germany.

#### Family ACCIPITRIDAE.

*Palaeoborus howardae* Wetmore, Proc. U. S. Nat. Mus., vol. 84, November 3, 1936, p. 73, fig. 13. Miocene: Dawes County, Nebraska.

---

[1] For the use of *Neocathartes* here see Wetmore, Auk, April, 1950, p. 235.

*Palaeoborus rosatus* A. H. Miller and L. V. Compton, Condor, vol. 41, no. 4, July 15, 1939, p. 156, fig. 34B. Lower Miocene: Rosebud beds, late Arikareean formation, Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

*Neophrontops dakotensis* Compton, Amer. Journ. Sci., ser. 5, vol. 30, October, 1935, p. 344, fig. 1. Lower Pliocene: Big Spring Canyon, 15 miles southwest of Martin, Bennett County, South Dakota.

*Neophrontops vetustus* Wetmore, Condor, vol. 45, no. 6, December 8, 1943, p. 229, fig. 62. Middle Miocene: Sheep Creek beds, Stonehouse Draw Quarry, Sioux County, Nebraska.

*Buteo antecursor* Wetmore, Bull. Mus. Comp. Zoöl., vol. 75, October, 1933, p. 298, figs. 1–5. Upper Oligocene: Brule beds, near Torrington, Goshen County, Wyoming.

*Buteo fluviaticus* A. H. Miller and C. G. Sibley, Condor, vol. 44, no. 1, January 15, 1942, p. 39, fig. 12. Middle Oligocene: Oreodon beds, on Owl Creek, 6 miles east of Carr, Weld County, Colorado.

*Buteo grangeri* Wetmore and Case, Contr. Mus. Pal. Univ. Michigan, vol. 4, no. 8, January 15, 1934, p. 129, 1 pl. Middle Oligocene: Oreodon beds, Big Badlands of Pass Creek, Washabaugh County, South Dakota.

*Miohierax stocki* Howard, Condor, vol. 46, no. 5, September 27, 1944, p. 236, fig. 40. Late Lower Miocene: Tick Canyon formation, near head of Vasquez Canyon, Los Angeles County, California.

*Spizaëtus willetti* Howard, Condor, vol. 37, no. 4, July 15, 1935, p. 207, fig. 40. Quaternary deposits (questionably of Pleistocene age): Smith Creek Cave, 34 miles north of Baker, White Pine County, Nevada.

*Palaeastur atavus* Wetmore, Condor, vol. 45, no. 6, December 8, 1943, p. 230, fig. 63. Lower Miocene: Lower Harrison beds, Stenomylus Quarry, about 2 miles southeast of Agate Springs fossil site, near Agate, Nebraska.

*Calohierax quadratus* Wetmore, Bull. Mus. Comp. Zoöl., vol. 80, no. 12, October, 1937, p. 429, figs. 1–3. Recent (prehistoric): Cave deposits on Great Exuma Island, Bahama Islands.

*Palaeoplancus sternbergi* Wetmore, Smithsonian Misc. Coll., vol. 87, no. 19, December 26, 1933, p. 12, figs. 1–19. Middle Oligocene: Upper Oreodon beds, east side of Plum Creek, Niobrara County, Wyoming.

*Sushkinia pliocaenica* Tugarinov, Trav. Inst. Palaezool. Acad. Sci. U. R. S. S., vol. 4, 1935, p. 89, fig. Pliocene: Irtush River, near Pavlodar, Kazakh S. S. R.

*Titanohierax gloveralleni* Wetmore, Bull. Mus. Comp. Zoöl., vol. 80, no. 12, October, 1937, p. 431, figs. 4–5. Recent (prehistoric): Cave deposits on Great Exuma Island, Bahama Islands.

Family Falconidae.

*Polyborus prelutosus prelutosus* Howard. *Polyborus prelutosus* Howard, Carnegie Inst. Washington, Publ. 487, July 7, 1938, p. 226, pls. 1–3. Pleistocene: Florida (Seminole Field in Pinellas County, and Melbourne), and California (McKittrick, Carpinteria and Rancho La Brea[1], Los Angeles).

*Polyborus prelutosus grinnelli* Howard, Condor, vol. 42, no. 1, January 19, 1940, p. 41. Pleistocene: San Josecito Cave, southern Nuevo León, México.

---

[1] Type locality.

*Falco oregonus* Howard, Carnegie Inst. Washington, Publ. 551, January 25, 1946, p. 178, pl. 1, figs. 2 3. Pleistocene: Fossil Lake, Oregon.

*Falco ramenta* Wetmore, Proc. U. S. Nat. Mus., vol. 84, November 3, 1936, p. 75, fig. 14. Miocene: Dawes County, Nebraska.

### Order GALLIFORMES.

### Family CRACIDAE.

*Ortalis tantala* Wetmore, Condor, vol. 35, no. 2, March 15, 1933, p. 64, figs. 10–14. Lower Miocene: Lower Harrison beds, Carnegie Hill, Sioux County, Nebraska.

*Ortalis pollicaris* A. H. Miller, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, no. 4, June 22, 1944, p. 91, fig. 5. Lower Miocene: Rosebud beds, late Arikareean formation, Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

### Family TETRAONIDAE.

*Tympanuchus stirtoni* A. H. Miller, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, no. 4, June 22, 1944, p. 92, fig. 6. Lower Miocene: Rosebud beds, late Arikareean formation, Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

### Family PHASIANIDAE.[1]

*Alectoris pliocaenica* Tugarinov, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 26, no. 3, January 30, 1940, p. 304, fig. 1. Pliocene: Near Odessa, Ukrainian S. S. R.

*Ammoperdix pontica* Tugarinov, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 26, no. 3, January 30, 1940, p. 304, fig. 2. Pliocene: Near Odessa, Ukrainian S. S. R.

*Colinus hibbardi* Wetmore, Univ. Kansas Sci. Bull., vol. 30, pt. 1, no. 9, May 15, 1944, p. 96, figs. 4–8. Upper Pliocene: Rexroad fauna, late Blancan age, Meade County, Kansas.

*Miortyx teres* A. H. Miller, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, no. 4, June 22, 1944, p. 93, fig. 7. Lower Miocene: Rosebud beds, late Arikareean formation, Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

*Cyrtonyx cooki* Wetmore, Condor, vol. 36, no. 1, January 15, 1934, p. 30, fig. 5. Upper Miocene: Upper Sheep Creek beds, 17 miles south of Agate, Sioux County, Nebraska.

*Pliogallus coturnoides* Tugarinov, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 26, no. 3, Jan. 30, 1940, p. 205, fig. 3. Pliocene: Near Odessa, Ukrainian S. S. R.

### Family MELEAGRIDIDAE.

*Meleagris crassipes* L. H. Miller, Condor, vol. 42, no. 3, May 15, 1940, p. 154, figs. 44 B, 45 A. Pleistocene: San Josecito Cave, Aramberri, Nuevo León, México.

---

[1] *Phasianus nicheti* "Gaillard" Bastin, Bull. Soc. Hist. Nat. Ardennes, vol. 28, no. 30, April, 1933, pp. 48, 53, 55, listed from the Pleistocene (Paleolithic) of Grotte de Nichet, Ardennes, France, is a nomen nudum without description or figure, based on bones identified by Gaillard as *Phasianus colchicus* Linnaeus.

Order GRUIFORMES.

Family GERANOIDIDAE.

*Geranoides jepseni* Wetmore, Condor, vol. 35, no. 3, May 15, 1933, p. 115, fig. 22. Lower Eocene: Greybull formation, South Elk Creek, Bighorn County, Wyoming.

Family EOGRUIDAE.

*Eogrus aeola* Wetmore, Amer. Mus. Nov., no. 711, April 7, 1934, p. 3, figs. 2–5. Upper Eocene: Irdin Manha formation, Chimney Butte, Shara Murun region, Inner Mongolia.

Family GRUIDAE.

*Grus conferta* A. H. Miller and C. G. Sibley, Condor, vol. 44, no. 3, May 15, 1942, p. 126, fig. 50. Late Lower Pliocene: Black Hawk Ranch, southern base of Mount Diablo, Contra Costa County, California.

*Sarcogeranus bogatshevi* Serebrovsky, Compt. Rend. (Doklady). Acad. Sci. U. R. S. S., vol. 27, no. 7, June 10, 1940, p. 767. Pleistocene: Kirov deposits, near Binagada, Baku, Azerbaijan.

*Palaeogrus geiseltalensis* Lambrecht, Nova Acta Leopoldina, vol. 3, no. 14, 1935, p. 361, pl. 1, fig. 1. Middle Eocene: Lutétian beds, Cecilie Mine, Mücheln im Geiseltal, Merseburg, Halle, Germany.

Family ARAMIDAE.

*Badistornis aramus* Wetmore, Journ. Morph., vol. 66, January 2, 1940, p. 30, figs. 7–10. Oligocene: Metamynodon zone, Brule beds, 35 miles southwest of Scenic, South Dakota.

*Gnotornis aramiellus* Wetmore, Smithsonian Misc. Coll., vol. 101, no. 14, May 11, 1942, p. 1, figs. 1–4. Oligocene: Protoceras – Leptauchenia beds, Upper Brule formation, 25 miles southeast of Scenic, 6 miles east of Rockyford, Washington County, South Dakota.

Family RALLIDAE.

*Telecrex grangeri* Wetmore, Amer. Mus. Nov., no. 711, April 7, 1934, p. 13, fig. 6. Upper Eocene: Irdin Manha formation, Chimney Butte, Shara Murun region, Inner Mongolia.

*Rallus prentici* Wetmore, Univ. Kansas Sci. Bull., vol. 30, pt. 1, no. 9, May 15, 1944, p. 99, figs. 9–19. Upper Pliocene: Rexroad fauna, late Blancan age, Meade County, Kansas.

*Epirallus natator* L. H. Miller, Univ. California Publ. Zool., vol. 47, no. 3, March 6, 1942, p. 43, fig. 1a. Pleistocene: San Josecito Cave, Aramberri, Nuevo León, México.

Family PHORORHACIDAE.

*Andrewsornis abbotti* Patterson, Field Mus. Nat. Hist., Geol. Ser., vol. 8, no. 8, October 31, 1941, p. 50, fig. 16. Oligocene: Deseado formation, Cabeza Blanca, Chubut, Argentina.

*Phororhacos rapax* (Kraglievitch). *Mesembriornis rapax* Kraglievitch, Ann. Soc. Cient. Argentina, vol. 142, pt. 3, September, 1946, p. 108, figs. 2–9. Middle Pliocene:

Chapadmal formation, near the mouth of Arroyo Lobería, Provincia de Buenos Aires, Argentina.

Family Cunampaiidae.

*Cunampaia simplex* Rusconi, Bol. Paleont. Buenos Aires, no. 21, May 2, 1946, (p. 1), fig. 1. Oligocene: Atala formation, 500 meters west of Mina Atala, Las Heras, Mendoza, Argentina.

Family Bathornithidae.

*Bathornis geographicus* Wetmore, Smithsonian Misc. Coll., vol. 101, no. 14, May 11, 1942, p. 3, figs. 5–13. Oligocene: Protoceras – Leptauchenia beds, Upper Brule formation, 25 miles southeast of Scenic, and 6 miles east of Rockyford, Washington County, South Dakota.

*Bathornis celeripes* Wetmore, Bull. Mus. Comp. Zoöl., vol. 75, October, 1933, p. 302, figs. 6–14. Upper Oligocene: Brule beds, near Torrington, Goshen County, Wyoming.

*Bathornis cursor* Wetmore, Bull. Mus. Comp. Zoöl., vol. 75, October, 1933, p. 310, figs. 15–19. Upper Oligocene: Brule beds, near Torrington, Goshen County, Wyoming.

Family Otididae.

*Chlamydotis pliodeserti* Serebrovsky, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 33, nos. 7–8, December 20, 1941, p. 474. Pliocene: Odessa, Ukrainian S. S. R.

Order Diatrymiformes.

Family Diatrymidae.

*Diatryma* (?) *cotei* Gaillard, Ann. Soc. Linn. Lyon, vol. 80, n. s., 1936 (March, 1937), p. 113, figs. 1–6, 8–10. Eocene: Slopes of Mont-d'Or, near Clôtre, Commune of Lissieu, Rhône, France.

Order Charadriiformes.

Family Rhegminornithidae.

*Rhegminornis calobates* Wetmore, Proc. New England Zoöl. Club, vol. 22, June 23, 1943, p. 61, pl. 11, figs. 1–5. Lower Miocene: Hawthorne formation, Thomas farm, 8 miles north of Bell, Gilchrist County, Florida.

Family Scolopacidae.

*Philomachus binagadensis* (Serebrovsky). *Machetes* (*Tringa?*) *binagadensis* Serebrovsky, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 27, no. 7, June 10, 1940, p. 767. Pleistocene: Kirov deposits, near Binagada, Baku, Azerbaijan.[1]

---

[1] Listed as *Philomachus binagadensis* by Serebrovsky in Compt. Rend. (Doklady) Acad. Sci. U. R. S., vol. 33, nos. 7-8, December 20, 1941, p. 473.

*Palnumenius victima* L. H. Miller, Univ. California Publ. Zoöl., vol. 47, no. 3, March 6, 1942, p. 45. Pleistocene: San Josecito Cave, Aramberri, Nuevo León, México.

*Totanus numenioides* Serebrovsky, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 33, nos. 7–8, December 20, 1941, p. 476. Pliocene: Odessa, Ukrainian S. S. R.

### Family STERCORARIIDAE.

*Stercorarius shufeldti* Howard, Carnegie Inst. Washington, Publ. 551, January 25, 1946, p. 184, pl. 2, figs. 1–2. Pleistocene: Fossil Lake, Oregon.

### Family LARIDAE.

*Gaviota niobrara* A. H. Miller and C. G. Sibley, Auk, vol. 58, no. 4, October, 1941, p. 563, fig. 1. Upper Miocene: Niobrara River Zone, Niobrara Game Preserve, Cherry County, Nebraska.

### Family ALCIDAE.

*Brachyramphus pliocenus* Howard, Carnegie Inst. Washington, Publ. 584, June 22, 1949, p. 191, pl. 3, figs. 1–2. Middle Pliocene: San Diego formation, Los Angeles Museum locality 1080, on Washington Boulevard Freeway, San Diego, California.

*Miocepphus mcclungi* Wetmore, Journ. Morph., vol. 66, January 2, 1940, p. 35, figs. 11–14. Miocene: Zone 12, Calvert formation, near the mouth of Parker Creek, Calvert County, Maryland.

*Mancalla diegense* L. H. Miller, Trans. San Diego Soc. Nat. Hist., vol. 8, December 15, 1937, p. 376, 2 figs. Upper Middle Pliocene: San Diego formation, Market Street near Euclid Avenue, San Diego, California.

## Order PSITTACIFORMES.

### Family PSITTACIDAE.

*Ara autocthones* Wetmore, Journ. Agr. Univ. Puerto Rico, vol. 21, no. 1, January, 1937, p. 12, pl. 1, figs. 8–9. Recent (prehistoric): Kitchen midden deposits at Concordia, southwestern St. Croix, Virgin Islands, West Indies.

*Protoconurus roosevelti* Spillmann, Proc. Eighth Amer. Sci. Congr., vol. 4, September 3, 1942, p. 381, figs. 1–9. Pleistocene: Peninsula of Santa Elena, Ecuador.

## Order STRIGIFORMES.

### Family PROTOSTRIGIDAE.

*Protostrix mimica* Wetmore, Proc. U. S. Nat. Mus., vol. 85, January 17, 1938, p. 27, figs. 4–5. Lower Eocene: Wasatch beds, south side of Ten Mile Creek, 12 miles northwest of Worland, Wyoming.

### Family TYTONIDAE.

*Tyto pollens* Wetmore, Bull. Mus. Comp. Zoöl., vol. 80, October, 1937, p. 436, figs. 10–14. Recent (prehistoric): Cave deposits on Great Exuma Island, Bahama Islands.

Family Strigidae.

*Strix brea* Howard, Condor, vol. 35, no. 2, March 15, 1933, p. 66, fig. 15. Pleistocene: Rancho La Brea, Los Angeles, California.

*Strix dakota* A. H. Miller, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, no. 4, June 22, 1944, p. 95, fig. 8. Lower Miocene: Rosebud beds, late Arikareean, Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

*Asio pigmaea* Serebrovsky, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 33, nos. 7–8, December 20, 1941, p. 476. Pliocene: Odessa, Ukrainian S. S. R.

Order Coraciiformes.

Family Bucerotidae.

*Geiseloceros robustus* Lambrecht, Nova Acta Leopoldina, vol. 3, no. 14, 1935, p. 365, pl. 2. Middle Eocene: Lutétian beds, Cecilie Mine, Mücheln im Geiseltal, Merseburg, Halle, Germany.

Order Passeriformes.

Family Icteridae.

*Pandanaris convexa* A. H. Miller, Condor, vol. 49, no. 1, February 6, 1947, p. 22, fig. 4 a–d. Pleistocene: Rancho La Brea, Los Angeles, California.

Family Fringillidae.

*Pipilo angelensis* Dawson, Condor, vol. 50, no. 2, March 16, 1948, p. 59, fig. 16. Pleistocene: Rancho La Brea, Los Angeles, California.

## Species eliminated from avian fossil list

Family Colymbidae.

*Podilymbus magnus* Shufeldt, from the Pleistocene of Fossil Lake, Oregon, proves to be based on the living species, *Podilymbus podiceps* (Linnaeus). See Wetmore, Proc. California Acad. Sci., vol. 23, no. 13, December 30, 1937, pp. 198–199.

Family Ardeidae.

*Ardea paloccidentalis* Shufeldt, from the Pleistocene of Fossil Lake, Oregon, was described from a fragmentary tarsometatarsus of the living species *Botaurus lentiginosus* (Montagu). See Howard, Carnegie Inst. Washington, Publ. 551, January 25, 1946, pp. 156–157.

Family Anatidae.

*Cygnus mathewi* Shufeldt, from the Pleistocene of Fossil Lake, Oregon, proves to be a synonym of the fossil *Cygnus paloregonus* Cope. See Howard, Carnegie Inst. Washington, Publ. 551, January 25, 1946, p. 159.

*Anser condoni* Shufeldt, from the Pleistocene of Fossil Lake, Oregon, likewise is a synonym of the fossil *Cygnus paloregonus* Cope. See Howard, l. c., p. 159.

Family CATHARTIDAE.

*Coragyps shastensis* (L. H. Miller), from Pleistocene cave deposits in California, is placed in the synonymy of the fossil *Coragyps occidentalis* (L. H. Miller). See Miller, L. H., Condor, 1941, pp. 140–141.

Family ACCIPITRIDAE.

*Aquila ferox* Shufeldt, from the Eocene of Wyoming, proves to be the claw of an edentate mammal. See Wetmore, Amer. Mus. Nov. no. 680, December 4, 1933, pp. 1–2.

Family PROTOSTRIGIDAE.

*Minerva antiqua* Shufeldt, from the Eocene of Wyoming, is also the claw of an edentate mammal. See Wetmore, l. c., pp. 1, 2.

Family CORVIDAE.

*Corvus shufeldti* Sharpe, from the Pleistocene of Fossil Lake, Oregon, is a synonym of the living *Corvus corax* Linnaeus. See Howard, Carnegie Inst. Washington, Publ. 551, January 25, 1946, p. 189.

Family ICTERIDAE.

*Euphagus affinis* Shufeldt, from the Pleistocene of Fossil Lake, Oregon, is a synonym of the living *Euphagus cyanocephalus*. See Howard, l. c., p. 189.

## Species of uncertain allocation

*Falco falconellus* Shufeldt, named from the Eocene of Wyoming, is relegated to *incertae sedis* since the type material includes fragments from at least 3 orders of birds and one mammal, none of which may be identified. See Wetmore, Proc. U. S. Nat. Mus., vol. 84, November 3, 1936, pp. 77–78.

*Urmiornis abeli* Lambrecht, Palaeobiol., vol. 6, pt. 2, 1938, p. 242, pl. 19. Pliocene: Upper level of lower Fars beds, Jebel Hamrin, Iran. The type of this species consists of three foot-prints, in reddish sandstone, that appear to be those of a wading bird. They are attributed to the crane genus *Urmiornis* because of *Urmiornis maraghanus* Mecquenem of the Lower Pliocene of Maragha, Iran, and as they are smaller are given a specific name, *abeli*. While the specimens studied by Lambrecht appear to be avian their allocation to family is deemed uncertain.

*Gryzaja odessana* Zubareva, Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., vol. 23, no. 6, June 13, 1939, p. 607, 1 fig. Middle Pliocene: from the Odessa "catacombs." Described from the distal part of a right tibio-tarsus, and from a second specimen of slightly larger size. It is said to have been a swimming bird, but a peculiar one without apparent relatives.

# Introduction to Swedish Ornithology

*Sven Hörstadius*

*Zoological Institute, Uppsala*

The main building of Uppsala University is of quite recent date, being built in the 1880's, but the university itself is a considerable age, having been founded in 1477. During the 17th, 18th and 19th centuries we can mention three persons, who have been particularly dominating figures and who have left their mark on the university during each of these centuries. In front of the university building there stands a statue of Erik Gustaf Geijer, Uppsala's great historian, philosopher, poet and composer during the 19th century. The 18th century was dominated by Carl von Linné. The great personage of the 17th century was Olof Rudbeck the elder (Olaus Rudbeckius).

Olof Rudbeck was an all-round scholar of exceptional capacity, who was active in many branches with a rare energy. As Professor of Medicine he improved the medical teaching and built a teatrum anatomicum under the dome, which we can still see to this day on the building between the cathedral and the university. He is most famous as the discoverer of the lymphatic system, at the same time and independently of Bartholin the Dane. He laid out two botanical gardens, one of which is the present academic botanical garden below the castle containing the botanical institutions, whilst the other is the garden which later belonged to Linné. He was an architect and master-builder, trained engineers, mining-engineers, surveyors, officers for fortifications, was our first field archeologist, was a musician and composer, and for many years the head of the university. He wrote a great fantastic work called "Atlantica", in which he wished to prove that Sweden was Plato's Atlantis and the place of origin of nearly all European culture. Mention may be made amongst his natural scientific works of "Campi elysii", containing thousands of pictures of every known plant. This was partly executed by Rudbeck himself, partly by his son, and partly by other draftsmen. Only two parts of this mighty work had been published, before the nearly seven thousand wood engravings were destroyed in the great fire at Uppsala in 1702.

When King Charles XI visited Uppsala in the year 1693, he was shown a number of illustrations of birds, executed by the son, Olof Rudbeck the younger. The King was so impressed by the pictures of the birds, that he gave financial assistance for a journey to Lapland planned by Rudbeck the younger and granted him permission to shoot birds wherever he wanted. It was also ordained that any rare birds, which were found, should be handed over to him.

Young Rudbeck made his journey to Lapland in the year 1695, later writing a description of it in twelve parts, of which eleven were destroyed in the fire of 1702. This loss is regrettable not only from a cultural historical but also from an ornithological point of view, as we can learn from the first part, which was saved, that Rudbeck was extremely interested in birds and was a good observer. Thus he describes the way the wryneck uses its long tongue, the crossbill's way of breaking up cones and so on. Sketches from his journey later gave material for a number of the many plates, which were produced especially during the next few years, 1696–1699, and which were assembled in a great collection of plates. The last to be executed dating from 1710. This collection of plates, which has not got any name, was never published, but Rudbeck himself made a copy, also in colour although it is not complete. Amongst other things all the water fowl are missing. The copy was made about 1720. In addition there is an example, copied in 1823 in black and white by G. J. Billberg, containing all the pictures in the original. These two copies belong to the library of Uppsala University. The original, the so-called De Geer or Löfsta example, was purchased in the 1730's by the entomologist Baron Charles De Geer of Löfsta, where it is still preserved. This magnificent work is displayed at the Congress, through the kindness of the present owner, Baron Louis De Geer.

The volume contains 272 pages, of which the first 55 show pictures of insects. A number of pages are bare and are not numbered. The greater part of the plates, which were first thought to be missing, have however been found lying in a large portfolio, containing 35 plates of larger size. Some of the species have been reproduced in several pictures. Altogether 122 species are represented in this collection of plates.

The plates appear to have been bound at a late date. The order having then been followed, which was given by numbers on the name slips written by Rudbeck, which accompanied the plates. On these slips references occur to earlier authors such as Gessnerus, Aldrovandus, Willoughby and Rajus. Rudbeck has not published any system, but the numerical order must be considered as giving his idea of the division of the birds. He seems to have been surprisingly before his time in this matter, because here warblers have undoubtedly been put first for the first time. After which the scansorial birds, doves, gallinaceous birds, crows, birds of prey, waders and water fowl follow. If an exception is made for the placing of the crows, this division is on the whole not unlike that, which was often used up to the end of the 19th century.

Rudbeck the younger was his father's successor as professor. In this capacity he gave lectures about birds. At that time there were no collections of stuffed birds. At these lectures the plates constituted the demonstration material. Some notes exist written by three auditors at the lectures in 1727–1729. These notes are by no means complete, but show us, however, that Rudbeck had acquired a not inconsiderable knowledge of the structure and habits of many birds.

We are fully justified in calling Rudbeck the younger the founder of ornithology in Sweden through his collection of plates, which were remarkable for his time, through his laying down of the system, which is expressed in the numbering of the pictures, and through his lectures.

One of the three auditors, whose notes from Rudbeck's lectures are preserved, was Carolus Linnaeus, who attended a number of them during 1728 and 1729. Birds are probably the only group of animals, about which Linné received instruction. They were also the group of animals, in which he felt the greatest interest. His sense of beauty was attracted by their lovely forms, colours and song. It was therefore birds, to which he devoted his first zoological work. It is indisputable that Rudbeck's work was of the greatest importance for its production. In the year 1730 Linné got a wonderful opportunity for studying the pictures of birds more closely, when he became tutor to Rudbeck's younger sons and was able to live in Rudbeck's house and make use of his library, which he did not neglect to do. As early as that year, at the age of 23, he wrote a little book about birds, in which he stated on the title-page, dated January 1st 1731, that it constitutes a catalogue of all Swedish birds, arranged in a new system according to the construction of their beaks. It is perhaps worth mentioning that this basis for division was obviously not the only one, which the young scientist had in mind. On the inside of the cover there is a note, which indicates that he had considered an arrangement according to the number of eggs in every species, "Monospermae, Dispermae etc.", a basis for division which he fortunately abandoned but which is typical for his endeavour to use numerical characteristics. The book is small, pocket size, and clearly much used. Many additions have been made later, on supplementary pages amongst others. This work, which he called "Methodus Avium Sveticarum", was never published during his lifetime but was printed for the 200th anniversary of his birth in 1907.

There is no doubt that Linné obtained the material for this work to a very great extent from Rudbeck's lectures and plates. He had not yet made many journeys in Sweden at that time and had, therefore, not been able to obtain any great experience himself of the bird world. Although he undoubtedly in certain cases builds entirely on Rudbeck, his work is independent in many respects. Rudbeck's collection of plates comprised 122 species. Methodus includes 197 numbers, but not only does the list contain a number of tame birds, but also some species have been included under several numbers, for which reason the number of wild Swedish birds amounts to about 170. The total thus considerably exceeds Rudbeck's, and yet at least eight of the birds have not been included, as Linné obviously did not think that he possessed sufficient knowledge about them.

The original manuscript has later been increased by new notes during the course of the years, new pages being glued into the book with references to descriptions of journeys amongst other things. The little book thus shows how Linné perpetually tried to increase his knowledge of birds.

Linné by no means follows Rudbeck as far as the system is concerned. It may also be queried whether Rudbeck had carried out his numbering at that time. Linné groups the birds in eight classes, with sub-divisions which he calls sections. Similarly to Aldrovandus he commences with the birds of prey. He also places parrots and owls in the same class. Then follow crows, small waders, large waders, water fowl, gallinaceous birds, scansorial birds and perching birds. Warblers and finches are thus placed last in the system.

One of the reasons for the weakness in the system in Methodus is that Linné based the division mainly on the construction of the beak alone, even if he also took into consideration such organs as the feet, the tongue and appendage on the head. He has made a series of drawings of these organs in Methodus. An advance as compared to his predecessors is that he exclusively employs morphological characteristics and does not base his system on the size of the birds or their circumstances of life.

In his later work, in different editions of Systema Naturae, the first of which appeared in 1735, Linné has aimed at concentration, which was obtained by means of amalgamations. In this way the previous classes, which are now called orders, were decreased from 8 to 6. The larger waders were combined with the lesser, and the crows with the scansorial birds (woodpeckers, tree-creepers, nuthatch) as well as cuckoos and hoopoes etc. to a very heterogeneous group. Another deterioration lay in the fact that the sub-divisions, the sections, were removed. Finally an unfortunate limitation of the number of genera was made. Thus were amalgamated, for instance, the genera of Grus, Ciconia and Ardea, which were included in Methodus, to one genus, Ardea. Cygnus, Anser and Anas were combined under the name of Anas. Linné thus seems more up-to-date in his maiden work than in the following, obviously depending on the fact that he there more closely followed Rudbeck's bird names, while his later amalgamations decreased the lucidity of the system.

In the year 1746 the first edition of Linné's Fauna Svecica appeared. The binomial nomenclature in zoology was introduced with the tenth edition of Systema Naturae 1758. Fauna Svecica is often quoted there, which in its turn refers to Rudbeck's pictures of birds. In many cases Linné's names of birds are based on Rudbeck's, in certain cases he only appears to have known the species from Rudbeck's plates. Consequently, a number of the pictures in that work constitute Linné's type specimen.

It can perhaps be of interest to mention in this connection, that Linné is the creator of the word Fauna. He seems to have spent a long time searching for an equivalent to the term Flora for the vegetable world and had thereby thought at an early stage of another classical god. A manuscript as yet unpublished, now in the possession of the Linnean Society, and probably dating from the beginning of the 1730's, deals with the European mammals and is called "Caroli Linnaei Pan europaeus etc.". As he was obviously not content with Pan as an equivalent to Flora he only calls his catalogue of Swedish animals, published in 1736, "Animalia per Sveciam observata". The new term was introduced with Fauna Svecica in 1746 and it has obtained a general standing. It refers to the wife or daughter of the god of forests and fertility Faunus.

It is not necessary to speak in detail here about Linné's valuable contribution to science. The Englishman Ray had created the idea of species. Through Linné's introduction of the ideas of genus, order and class as well as the binomial nomenclature, it became possible to arrange and survey the innumerable quantities of forms of life. His sexual system and other systematic forms for division became the foundations of botany. The zoological systematics as well were greatly advanced thanks to him, even if his contribution here is not of the same degree as in botany. He is, in addition, very well-known to us owing to his descriptions of journeys, in which he appears, similarly to his acute biological perception, as one of the most acute observers throughout the ages. Through these descriptions of journeys he is also considered as one of our most famous authors.

Linné's greatness is not lessened by the fact that his contribution to ornithology was not of such an epoch-making nature as his contribution to botany. First and foremost we think of him as the great name-giver and classifier of plants and animals. We must not forget, however, that his acute powers of observation were not limited to the study of external morphological characteristics alone. He has had, amongst other things, a keen eye for that strange phenomenon, the migration of birds, and has made observations in the matter. He touched on the problem in lectures in 1748 and urged his auditors to send their observations in this matter to the Royal Academy of Science. The question is treated in greater detail in C. D. Ekmarck's doctor's thesis in 1757. Nowadays the doctor in spe writes his own thesis, at that time it was written by the teacher and defended by the future doctor. Such a work is the treatise on Migrationes Avium.

Linné first states what some authors have said concerning the migration of foreign birds and then gives an account of the migratory habits of about one hundred Swedish birds. It is curious that he does not consider it unlikely that wrens and swifts hide under stones and in hollow trees during the winter. He rejects the old belief that the stork should pass the winter at the bottom of the sea, but faced with the great quantity of apparently reliable information that swallows spend the winter in the same way, he is unable to free himself from this superstition. Otherwise it is remarkable in how many cases Linné knew about the migratory ways, although he is conscious of the gaps in his knowledge in "this very obscure question". In order to remedy this he emphasizes the importance of international co-operation. Attention should be given to these problems in different parts of the globe and the observations should be communicated to the world of science. Notes should be made in southern Spain, Italy and Constantinople about which birds pass by there and the date this occurs. By this means Linné had already indicated some of the most important migratory routes in Europe. Regarding the reasons for migration he draws attention to the fact that cold, which gives rise to a shortage of food, is the cause for the birds flying away. Certain water fowl only move far enough to find open water. Our summer with its wealth of insects, protective forests and long days tempts them with good conditions for breeding, in addition to which fondness for their native tracts and habit also contribute to the reasons for the birds' return.

Before we continue, after these glimpses of Linné as an ornithologist, to his successor it can perhaps be the right moment to mention a little of what we have preserved in the way of relics from his life and work here in his own town. It is a matter of common knowledge that Linné's collections and manuscripts were sold to England, where they are now conserved in an exemplary way by the Linnean Society. Here in Uppsala the house, where he lived in later years and where he died, has been taken over by the Swedish Linnean Society, which has collected there everything it could find of the family's possessions. The garden belonging to the house, which as I said previously was laid out by Rudbeck the elder, has been restored to correspond exactly with the way it looked in Linné's day, thanks to a contemporary picture, which indicates the way the plants were placed in the garden. Then we have Linné's charming summer residence, Linné's Hammarby, to which one of our excursions has been arranged. Linné is buried under the floor of the Cathedral.

The two Rudbecks, father and son, established the first natural history museum at Uppsala, but it was completely destroyed during the great fire of 1702. Shortly afterwards interested persons began to collect material for a new museum, which was assembled by the skilful anatomist and teacher, Professor Lars Roberg, in 1710 in a museum connected with the Academic Hospital. We know that Linné saw these collections, because he mentions in a letter that he had seen a snake there with two heads as well as a "Lacerta volans s. Draco". We know that among the birds was a stuffed cassowary. The collections were broken up shortly after Roberg's death. In the meantime, however, interest had arisen during the 18th century for collecting natural history specimens. Both royalty and rich private persons acquired natural history collections. The zoological collection of the University was started during Linné's time through the following donations:

1) from the Chancellor of the University Count Carl Gyllenborg, 1744, "Donatio Caroli Gyllenborg", described by Linné in his treatise Amphibia Gyllenborgiana, 1745.

2) from the Hereditary Prince, later King Adolph Fredrik, 1745, "Donatio Adolphi Friderici", described by Linné in 1746 under the name of Museum Adolpho-Fridericianum (in Ammoenitates Academicae called Museum Principis).

3) from Ironmaster Claes Grill, 1747, "Donatio Claudii Grill", described by Linné in 1748 under the title of Surinamensia Grilliana.

4) from the Director of the East India Company Magnus Lagerström, 1748, "Donatio Magni Lagerström", described in Linné's treatise Chinensia Lagerströmiana, 1754.

In addition there was a large collection with different origins, in which was included a gift from Mercantile Counselor Jonas Alströmer, 1749. This collection has been called "Donatio Jonae Alströmer nec non Caroli Linné", and the species included in it are described by Linné in the 10th and 12th editions of Systema Naturae.

The collections first received were kept the first years in a room on the upper floor of the Prefect's residence in Hortus Botanicus (the so-called Linné Garden, laid out by Rudbeck the elder) but were moved in 1747 to the southern part of the orangery building in the same garden. The greater part of what now remains of these collections has been placed in the same room in the Linné House, where they were kept until 1747, while a lesser part is displayed in a glass case in the Museum of the Zoological Institute.

Finally it can be mentioned that King Gustav IV Adolf presented a natural history collection called "Donatio Gustavi Adolphi" to the university in 1803. This collection, which was described by Linné in 1764 in a magnificent volume called "Museum Ludovicae Ulricae Reginae", comprises a great number of insects, corals and molluscs and is preserved in its entirety in the Zoological Institute.

The establishment of the Zoological Museum and the Zoological Institute at the University of Lund dates back to 1735, when Professor Kilian Stobaeus, well-known in our scholastic history, presented his natural history collection to the university. Stobaeus was Linné's teacher during his stay at Lund from 1727 to 1728, but it is hardly probable that Linné learnt much of ornithological value, as Stobaeus's interests chiefly were devoted to mineralogy.

Lund played a very important part in the development of ornithology in Sweden after Linné, thanks to Sven Nilsson (1787–1883), who lived and worked in that town. Ever since Linné's day botany had occupied the place of honour in Sweden. Through Sven Nilsson zoology obtained a less obscure and more independent position. He acquired a remarkable knowledge of the Swedish vertebrate animals and their habits and gave us with his Skandinavisk Fauna (1820–1855) the first real fauna, even describing the animals' occurrence and way of living. Due to the fact that it was written in Swedish and not only intended for zoologists but also for sportsmen it had a wide circulation, not only in Sweden but in the whole of Scandinavia.

Sven Nilsson made even greater contributions to science in other spheres. He was the first person to point out the fossilization of plants and animals in Swedish rocks. He assembled an extremely valuable collection of subfossil bones from peat-bogs in Skåne and made deductions from these bones about the history of the immigration of our animal world, whereby he also made use of his brilliant observations regarding the rising and falling of our land and the extent of the inland ice. Our fauna consists, according to Nilsson, of a group of animals, which came from the south, when Skåne was joined to the Continent, and a group, which came from the north from Finland and Russia.

Nilsson is, however, most famous as one of the great names in archaeological research and comparative ethnography, perhaps one might even say the actual founder of that science. His epoch-making ideas about the stone and bronze ages were presented, curiously enough, for the first time in the introduction to the 2nd edition of the bird fauna "Utkast till jagtens och fiskets historia på Skandinavien".

Even if Sven Nilsson has not meant so much, from an international point of view, for the development of ornithological science, I have considered it necessary to mention his work in some detail. His Fauna was of the greatest importance, not only for us in Sweden but also for the whole of Scandinavia, as it was the first of its kind. His ideas about the immigration of our fauna were epoch-making. As an archaeologist he was a pioneer for a new branch of science. Sven Nilsson is undoubtedly one of our great scientists.

Even if none of our subsequent ornithologists can be considered as really great, there are some which deserve to be mentioned here.

C. J. Sundevall (1801–1875) was from 1839 curator of the Vertebrate Section of the National Natural History Museum. He commenced the publication of a comprehensive bird fauna, Svenska foglarna, the first complete bird fauna with coloured pictures of all birds to be issued in Sweden. Through his anatomic studies he was led to take what was a remarkable step for that time, namely to place the warblers (Oscines) first in his system. It was not until later that he discovered to his astonishment, that the same standpoint had already been adopted by Rudbeck the younger. In "Svenska foglarna" an account is given of an interesting investigation about a migratory bird's route. We have seen that Linné had already studied the question of the migratory birds' ways, but a long time elapsed before he obtained any successors. A paper written by the Rev. C. Ulr. Ekström in 1826 about the migratory birds' dates of arrival and departure in the Province of Södermanland, based on series of observations during the course of 15 years, is also of importance. He could show that the date of arrival for many species only varies very inconsiderably year by year. He also delivers the opinion that every species has its own migratory routes, even if these can be altered to a greater or lesser extent in certain circumstances. Regarding the reasons for migration he emphasizes amongst other things the importance of instinct. The question of the routes used in migration was now taken up by Sundevall, who realized the importance of carefully investigating every species' migratory route in order to be able to penetrate at all into the problem of the migration of birds. He selected cranes as the subject of his investigation, as they migrate by day and are well-known and easy to observe. By recruiting the help of persons interested in birds in many countries, particulars were obtained of the way the cranes take on their flight. In this manner real knowledge was attained for the first time of the exact route taken by a species when migrating. Thanks to this investigation Sundevall appears as a forerunner to the Finlandic zoologist J. A. Palmén, who published inthe year 1874 a treatise called "Om foglarnas flyttningar", which has been of great importance for future research work about migratory birds.

Gustav Kolthoff (1845–1913) was not an academician but a taxidermist, working during his later years at the Zoological Institute here in Uppsala. He is the creator of the great Biological Museum in Stockholm as well as the little Biological Museum here in Uppsala, in which the higher Swedish land animals are shown in their natural surroundings in an excellent way. He was a remarkable authority on birds and their habits and famous as an extremely crack shot. He has written a number of descriptions of nature and animals, in addition to which he published together with L. A. Jägerskiöld the distinguished work "Nordens Fåglar" (1895–1899). This work has undoubtedly to a considerable degree contributed to arousing interest for the study of birds among numerous young people, who are attracted by biology.

Kolthoff's collaborator in Nordens Fåglar, L. A. Jägerskiöld (1867–1945), was the Curator of the Natural History Museum in Gothenburg, which he made a centre for zoological research in Western Sweden. In addition to his collaboration in Nordens Fåglar it should be specially emphasized that the ringmarking of birds was begun in Sweden in 1911 on Jägerskiöld's initiative. The Museum at Gothenburg has taken a very active part in marking ever since. Up to the present date 227 946 birds have been ringed and of these 6 150 recoveries have been made. The results are published by the Museum at Gothenburg in Göteborgs Musei Årstryck.

A forceful personality was Professor Einar Lönnberg (1865–1942), the Curator of the Vertebrate Section of the National Natural History Museum 1904–1933. No Swedish zoologist since Linné has mastered in a systematic respect so many large classes of animals as Lönnberg. His enormous production not only covers fishes, reptiles, birds and mammals but even cetaceans, tape-worms and cephalopods etc. He personally worked to a great extent through the gigantic collections obtained from expeditions to Florida, the Caspian Sea and British East Africa. Mention should be made amongst his animal geographical works of "Origin of the North American Ornithic Fauna" (1928) and "The Development and Distribution of the African Fauna in Connection with Climatic Changes" (1929), thus dealing with animal geographical problems within such widely separated parts of the world as North America and Africa. Among his more popular works can be named a short fauna in three volumes dealing with Sweden's vertebrates

(Sveriges Ryggradsdjur, 1914–15) as well as the magnificent book Svenska Fåglar, illustrated with coloured plates executed by the von Wright brothers in Finland about 1820–30. Of very great importance was a magazine he started in 1906 called Fauna and Flora, which became, as the initiator had intended, a link between the research-workers and the nature-minded general public, who could there publish their observations concerning the habits and distribution of animals. Birds have occupied a very favoured position in this magazine. Lönnberg has also been of much consequence as our greatest biological authority in questions concerning the making of game-protection laws. He occupied a leading position in nature protection in Sweden and has actively contributed to the establishment of many of our national parks. Not least has he held a respected position within The International Committee for Bird Preservation, and we remember that he took the initiative in promoting Wildfowl Research as a basis for international bird preservation.

Other distinguished workers in avian systematics and avian geography are Nils Gyldenstolpe, expert on tropic and subtropic birds, Hugo Granvik, who has described his collections from East Africa, and Sten Bergman, explorer in North Eastern Asia and New Guinea.

We owe our basic knowledge of the distribution of birds in our mountains to Professor Sven Ekman, Uppsala, who is particularly known as author of the extremely valuable work "Djurvärldens utbredningshistoria på Skandinaviska halvön" (History of Animal Distribution in Scandinavia).

The first Swedish book illustrated with photographs of wild birds was published in 1912 by Dr. Paul Rosenius ("Min jakt med kamera"). Rosenius was soon followed by Bengt Berg, who is widely known for his beautiful books on Swedish birds and the animal life of Africa and India. Since then a great number of skilful photographers of birds have appeared. An exhibition of Swedish bird photographs of today is during the Congress arranged in the entrance lobby of the university.

During the last ten years ornithology in Sweden has made considerable progress through a group of young bird-investigators with a more ecological outlook. It is first and foremost the prominent field ornithologist Erik Rosenberg's activities, which have aroused interest. This group has its forum in Sveriges Ornitologiska Förening and its magazine Vår Fågelvärld. The association, which is only 5 years old, has already about 1 500 members and has built a station for bird migration research at Ottenby on the southern point of Öland. I mentioned that ringmarking in Sweden was started by Jägerskiöld at Gothenburg. From the year 1913 the National Natural History Museum in Stockholm, on the initiative of its present Curator, Professor

Hialmar Rendahl, has carried on extensive ringing, which 1913–1949 has resulted in 316 774 markings and 7 125 recoveries. Sveriges Ornitologiska Förening has also started ringmarking on a big scale at Ottenby, with assistance the last few years from Statens Naturvetenskapliga Forskningsråd. Last year's result, 14 059 ringed specimens, is an extremely high figure for a restricted locality. In addition I should especially like to draw attention to Gustaf Rudebeck's studies of migratory birds at Falsterbo as well as Sigfrid Durango's, Per Olof Swanberg's and Gunnar Svärdson's ecological studies.

This young group feels extremely honoured and grateful to have been given the task of organizing the 10th International Ornithological Congress.

## References

Areschoug, J. E., 1879. Minnesteckning öfver Carl Jacob Sundevall. K. Sv. Vet. Akad., Stockholm, 1879.

Linnæus, C., 1748–1752. Linnés föreläsningar öfver djurriket. (Edited by Einar Lönnberg.) Uppsala 1913.

— – 1757. Migrationes Avium. Svensk översättning av C. A. Brolén. Inledning och kommentar av Einar Lönnberg. Svenska Linnésällskapets Årsskrift XVIII; 23, 1935.

—— Methodus Avium Sveticarum. Edited by Einar Lönnberg. Inbjudning till Fil. Doktorspromotionen i Uppsala domkyrka den 24 maj 1907. Also issued in Uppsala Universitets Årsskrift 1907, Linnéfest-Skrifter, bd. 2, nr. 5.

Lönnberg, Einar, 1930. De Rudbeckska fågelbilderna och deras betydelse. Rudbecksstudier. Festskrift vid Uppsala Universitets minnesfest 1930; 211.

—— 1932. Linnaei anteckningar efter Olof Rudbeck d. y:s föreläsningar om svenska fåglar. Svenska Linnésällskapets Årsskrift XV; 41.

Lönnberg, Einar & Aurivillius, Chr., 1907. Carl von Linné såsom zoolog. In: Carl von Linnés betydelse såsom naturforskare och läkare. Uppsala. German edition in: Carl von Linnés Bedeutung als Naturforscher und Arzt, Jena 1909.

Nilsson, Sven, see below "Handbooks on Swedish Birds".

Nybelin, Orvar, 1946. Fauna Svecica 200 år. Svenska Linnésällskapets Årsskrift XXIX; 63.

Retzius, Gustaf, 1901. Sven Nilsson. Lefnadsteckningar öfver Kongl. Svenska Vetenskaps Akademiens efter år 1854 aflidna ledamöter. Bd. 4, hft 2; 35.

Rudebeck, G., 1950. Studies on bird migration, based on field studies in Southern Sweden. Suppl. I to Vår Fågelvärld.

Sundevall, Carl J., 1872. Om Rudbecks fogelbok. K. Wetenskaps Societeten i Uppsala Nova Acta, Ser. III, vol. 8, no. 7.

Swederus, M. B., 1896. Lars Roberg och Olof Rudbeck den yngre, Sveriges första zoologer. Zoologiska studier. Festskrift Wilhelm Lilljeborg tillegnad. Uppsala.

Uggla, Arvid Hj., 1950. När Linné införde namnet Fauna. Svenska Linnésällskapets Årsskrift XXXII 1949; 65.

## Handbooks on Swedish Birds

Carlson, A., 1894. Sveriges fåglar. Korta beskrifningar jämte redogörelse för deras lefnadssätt, häckzoner och flyttningstider. Lund.

Ekman, S., 1922. Djurvärldens utbredningshistoria på Skandinaviska halvön. Stockholm.

Holmgren, A. E., 1867–1871. Handbok i zoologi för lantbrukare, skogshushållare, fiskeriidkare och jägare. Part II, Skandinaviens Foglar. Stockholm.

Holmström, C. T., Henrici, P., Rosenberg, E. & Söderberg, R., 1942-1947. Våra Fåglar i Norden, I—IV. Stockholm.

Jägerskiöld, L. A. & Kolthoff, G., 1911–1926, 2nd rev. ed. (1st ed. 1898). Nordens Fåglar. Stockholm.

Lönnberg, E., 1915. Sveriges ryggradsdjur. Part II, Fåglarna. Stockholm.

Nilsson, S., 1817. Ornithologia Suecica. Havniae.

—— 1858, 3rd (4th) rev. ed. (1st /2nd/ ed. 1824–1828). Skandinavisk Fauna. Part II, Foglarna. Lund.

Pehrson, T. *and others*, 1930. Sveriges Djurvärld. Stockholm.

Rendahl, H., 1949, 4th rev. ed. (1st ed. 1935). Fågelboken, Sveriges fåglar i ord och bild. Stockholm.

Rosenius, P., 1913 (1946). Sveriges fåglar och fågelbon. No. 1-248. Lund.

Söderberg, R., 1948–1950, 6th–14th rev. ed. (1st ed. 1932-1934). Våra fåglar och hur man känner igen dem. I–IV. Stockholm.

Söderberg, R., Armington, S., & Lundin, H., 1951. Alla nordens fåglar. Stockholm.

af Ström, I. A., 1839. Svenska Foglarna, uppställda i systematisk ordning, med namn och korta kännemärken, till vägledning för Jägare och Jagtälskare. Stockholm.

Sundevall, C. J. & Kindberg, J. G. H., 1856-1886. Svenska foglarna. Stockholm.

Sveriges Ornitologiska Förening, 1951, 2nd rev. ed. (1 st ed. 1949). Förteckning över Sveriges fåglar. Stockholm.

Svärdson, G., & Durango, S., 1951. Svenska djur. Fåglarna. Stockholm.

Ursing, B., 1951. Däggdjur och fåglar. Stockholm.

von Wright, M., W., F. & Lönnberg, E., 1917–1929, new ed. (1st ed. 1828–1838, M. & W. von Wright). Svenska Fåglar, efter naturen och på sten ritade, med text av professor Einar Lönnberg. Stockholm.

## Bird Collections in Sweden

Sweden has several important museums and collections of natural history. The foremost ornithological museum is the Vertebrate Department of the National Museum of Natural History in Stockholm. Fine collections are also to be found in the University Museums at Uppsala and Lund, in the Natural History Museum at Gothenburg, in Malmö Museum, and in the Ornithological Museum at Jönköping. It should also be mentioned that especially the Swedish fauna is often richly represented in many high school museums in provincial towns.

The collections at the National Museum of Natural History date back to the year 1739, but it was first in the 1770's that ornithological collections began to be given to the museum. As late as the year 1808 the ornithological collection included only 430 specimens. In the year 1842 it had grown to approx. 5 200 specimens, of which the greater part were mounted. At the turn of the century the collections amounted to approx. 16 500 specimens. In the year 1920, five years after the removal to the new museum buildings, approx. 2 500 Swedish and approx. 6 000 foreign birds were placed on exhibition in the display collection while the main collection of skins included 3 000 Swedish and 23 000 foreign specimens, in addition to which the egg collection amounted to approx. 7 000 clutches. By 1950 the main collection of skins had grown to approx. 105 000 specimens. The Curator of the Vertebrate Department is Professor H. Rendahl, while Count N. Gyldenstolpe is primarily in charge of the ornithological collection.

As it can be of value to learn from what parts of the world Swedish museums own major (more than 100 specimens) collections, such a table is given here, the date of collection as well as the collector's name being given as a rule.

The National Museum of Natural History (Naturhistoriska Riksmuseet), Stockholm:

Africa: c. 250 specimens from S. Algeria, 1910 (N. Gyldenstolpe and P. Rosénius); c. 1 300 specimens from Egypt, Sudan, Sinai, Rhodos, 1832–1837 (J. Hedenborg); c. 360 specimens from Sudan, 1853 (Bartolucci); c. 150 specimens from Sudan, 1862 (Freyer); >150 specimens from Sudan, 1910 (E. von Rosen), 1913 (J. G. Wibom); 187 specimens from Eritrea, 1910 (K. G. Rodén); c. 400 specimens from The Gold Coast, 1935 (W. Lowe); c. 400 specimens from Kamerun, 1890 (Y. Sjöstedt), 1884–1885 (K. Knutsson and G. Waldau); 326 specimens from Belgian Congo, 1905 (K. E. Laman), 1931–1936 (J. Aspenlind); 2 180 specimens from E. Belgian Congo, 1913–1914 (E. Arrhenius), 1920–1921 (N. Gyldenstolpe); 1 546 specimens from former German East Africa, 1905–1906 (Y. Sjöstedt); 1 256 specimens from Kenya Colony, 1911, 1914 (E. Lönnberg and Prince Wilhelm of Sweden); 174 specimens from Kenya Colony, 1949 (B. Lundholm and Å. Holm); 1 333 specimens from Mt Elgon and Kenya Colony, 1920–1921 (H. Granvik); 114 specimens from S. W. Africa, 1880 (A. W. Eriksson); c. 220 specimens from Damaraland, Lake Ngami, 1854–1856 (J. A. Wahlberg); c. 200 specimens from Damaraland, 1876 (G. de Vylder); c. 2 600 specimens from South Africa, 1839–1845 (J. A. Wahlberg); c. 550 specimens from South Africa, 1854 (J. F. Victorin); 360 specimens from Madagascar, 1911 (W. Kaudern), 1929 (B. Ljungqvist); 166 specimens from Madagascar, 1879–1881, (Hildebrandt; bought by Otto von Zedlitz); 254 specimens of the genus Cisticola, 1928 (H. Lynes); 7 815 specimens from Tunisia, S. Algeria, 1912–1913; S. Somaliland, 1911; Senegal, 1908; Eritrea, 1908; Ethiopia, 1908; Angola, 1905–1906; etc. (O. von Zedlitz).

North America: c. 300 specimens from Greenland, 1899 (A. G. Nathorst), 1900 (G. Kolthoff), 1909 (A. Klinckowström), (C. Bangert etc.); > 100 specimens from Vancouver, 1862 (A. T. P. Cronhielm); c. 250 specimens from U. S. A., 1930 (M. Hachisuka); c. 360 specimens from Wisconsin, U. S. A., 1861 (T. Kumlien); c. 150 specimens from Texas, U. S. A., 1892 (B. Armstrong); > 100 specimens from Mexico, 1843 (D. S. Högberg), 1861 (A. Sallé); c. 800 specimens from Central America (Nicaragua, Panama, Costa Rica), 1882–1884 (C. Bovallius); c. 200 specimens from Guatemala (S. Ascoli); c. 250 specimens from The West Indies, 1945 (exchange from Museum of Natural History, Chicago); 231 specimens from Cuba, 1908–1919 (O. Tollin); 207 specimens from Haiti, 1928–1929 (E. L. Ekman); c. 160 specimens from Porto Rico, Haiti, Honduras, 1852–1867 (J. A. Hjalmarsson); 140 specimens from St. Bartholomew, 1865–1867 (A. Goës).

South America: c. 1 800 specimens from Colombia, 1931–1947 (K. von Sneidern); c. 200 specimens from Venezuela, 1848 (gift from King Gustav V of Sweden); c. 250 specimens from British Guiana, 1905 (C. Bovallius); c. 300 specimens from Surinam, 1861 (Barnet-Lyon); 9 452 specimens from Ecuador, 1910–1923 (L. Söderström); c. 200 specimens from Brazil, 1832 (Holm); 128 specimens from Brazil, 1833 (Godenius), 1925 (D. Melin); 13 224 specimens from Brazil, 1935–1937 (A. M. Olalla); c. 1 200 specimens from E. Brazil, 1815–1817 (L. Westin); 9 287 specimens from Bolivia, 1937–1939 (A. M. Olalla); > 100 specimens from Argentina, Bolivia, 1901–1902 (E. Nordenskjöld and G. von Hofsten); c. 350 specimens from Argentina, 1887 (H. Åberg); 1 048 specimens from Paraguay, 1946–1947 (C. Olrog); c. 140 specimens from Chile, 1854 (Bahlsen); c. 150 specimens from Chile, 1862 (R. A. Philippi); > 100 specimens from Chile, 1874 (V. Bustillos); c. 800 specimens from Chile, Tierra del Fuego, 1939–1940 (C. Olrog); c. 200 specimens from Juan Fernandez Islands, 1917 (K. Bäckström).

Asia: > 100 specimens from Siberia, 1876 (the Swedish Jenisej-expedition); c. 150 specimens from N. E. Siberia, 1879 (the Swedish Vega-expedition); c. 250 specimens from Transbaikalia, 1907–1908 (O. Bamberg); c. 700 specimens from Sakhalin, 1905–1906 (I. Ijima); c. 1 100 specimens from Kurile Islands, 1930–1939 (S. Bergman); c. 700 specimens from Kamchatka, 1920–1922 (S. Bergman); > 100 specimens from S. Georgia, 1902 (E. Sörling); c. 150 specimens from Persia, 1914 (R. Nicolin); 732 specimens from China, Mongolia, 1922–1930 (J. G. Andersson); c. 1 200 specimens from Korea, 1937 (S. Bergman); > 1 100 specimens from Japan, Formosa, Korea, 1930 (M. Hachisuka); c. 250 specimens from Central Asia, Kansu, 1930–1932 (Sven Hedin-expedition); 458 specimens from Kansu, 1921 (D. Sjölander); c. 200 specimens from Burma, 1877 (O. Limborg), 1934 (R. Malaise); 3 750 specimens from Siam, Malacca, 1911–1912, 1914–1915 (N. Gyldenstolpe and E. Eisenhofer); 2 263 specimens from French Indo-China, 1937–1939 (B. Björkegren); c. 700 specimens from Malacca, Borneo, Sumatra, 1916–1920 (Museum in Kuala Lumpur; bought by F. Adelborg); c. 200 specimens from Philippine Islands, 1890–1892 (M. J. Franzén); c. 150 specimens from Java, 1823 (van der Capellen); c. 230 specimens from Java, 1843 (Hjärne); > 100 specimens from Java, Moluccas, 1826 (gift from King Gustaf V of Sweden).

Australia: c. 1 200 specimens from N. W. Australia, 1910 (E. Mjöberg); c. 130 specimens from N. Queensland, 1889 (C. Fristedt); > 100 specimens from New South Wales, 1878 (R. Söderberg); c. 1 300 specimens from New Guinea, 1949 (S. Bergman).

Europe: > 200 specimens from Spitsbergen, 1864, 1868, 1873 (Swedish expeditions); > 100 specimens from Russia, 1848 (Lilljeborg), 1872 (W. Meves); c. 1 500 specimens from The Kola Peninsula, 1876–1878 (H. af Sandeberg); c. 200 specimens from S. E. Ural, Russia, 1872 (W. Meves); c. 130 specimens from Macedonia, 1918 (München Museum); c. 200 specimens from Cyprus, 1947 (G. Mavromonstakis).

C. 1 400 specimens from the circumnavigation of the globe of the frigate "Eugenie" 1851–53.

C. 1 000 specimens from Museum Paykull, 1819.

C. 700 specimens from Museum Grill, 1829.

The Lund University Zoological Museum: South Africa, especially Damaraland, 429 specimens 1866 (Charles John Andersson, discoverer of Lake Ngami). 398 specimens from Wisconsin, U. S. A., collected in the middle of the 19th century by Kumlien. Chile 120 specimens 1948–49 (Erik Dahl). 429 specimens mainly from India, 1845 (Axel Gustaf Gyllenkrook). 94 specimens from the Faeroes, presented 1905 by Dr. Jörgensen, Thisted.

The Uppsala University Zoological Museum has extensive display collections of native and foreign birds but no major collection of skins. These have instead been handed over to the National Museum of Natural History.

The Natural History Museum, Gothenburg (Naturhistoriska Museet, Göteborg):

Africa: 182 specimens from Sudan, 1920 (W. Pekkala); 203 specimens from Kamerun, 1891–1892 (Y. Sjöstedt); 69 specimens from Portuguese W. Africa, 1948–1949 (D. Sjölander); 218 specimens from British S. Africa and Portuguese W. Africa, 1912–1913 (H. Skoog); 141 specimens from Damaraland, 1875–1880, 1885 (A. W. Eriksson); 431 specimens from Namaqualand, Damaraland, 1856–1863 (Ch. Andersson).

North America: 104 specimens from North America, 1876 (O. Dickson, Ch. Weinberg); 68 specimens from E. Greenland, 1936–1937 (M. Råum); 83 specimens from E. Greenland, 1921–1922 (E. Lehn-Schiøler); 72 specimens from S. Greenland, 1909 (O. Nordenskiöld, H. Skoog); 102 specimens from Nicaragua, 1882, 1883, 1892, 1896 (B. Bovallius).

South America: 335 specimens from S:ta Fe de Bogota, Colombia, 1871 (N. Pereira); 2 719 specimens from Ecuador, 1885, 1886, 1900–1927 (L. Söderström); 548 specimens from Rio Tena, Province Pichincha, Ecuador, 1917 (R. Karsten); 118 specimens from Bahia, Brazil, 1842–1845 (D. Lindgren); 195 specimens from Montevideo, Uruguay, 1840–1842 (J. Tarras).

Asia: 853 specimens from the Chinese Provinces of Kiangsu and Anhwei, 1921–1922 (K. Kolthoff); 149 specimens from Sakhalin, Japan, 1914 (L. Munsterhjelm); 165 specimens from Malacca, Anamba Islands (Nyman?); 91 specimens from Borneo, 1923 (E. Mjöberg).

Australia: 101 specimens from Gympie (North of Brisbane), Queensland, 1870–1891 (A. E. Sundberg).

147 specimens from Iceland, Faroe Islands, Greenland, 1912–1913, 1923 (G. Dinesen).

95 specimens from the Swedish Polarexpedition 1868 (A. E. Nordenskiöld).

Malmö Museum has mainly gone in for display collections. The Museum has, however, approx. 3 000 skins from Kenya, East Africa (Mount Elgon, Turkana, Kikju), collected by Hugo Granvik 1925–27 and 1928–31.

# Speciation in Birds

## Progress Report on the Years 1938—1950

*Ernst Mayr*

*The American Museum of Natural History, New York*

To discuss species and speciation in Uppsala seems particularly appropriate for the name Linnaeus is in the mind of every biologist inseparably linked with the words species and Uppsala. It was Linnaeus who placed taxonomy on a solid foundation through the introduction of binomial nomenclature. On this foundation it has prospered and grown into the large field it is today. However, there is a great difference between the systematics of 1758 and that of 1950. Whereas Linnaeus knew only 564 species of birds, we now know 8 600. But, more important, the emphasis in the days of Linnaeus was on the discovery of new species, their description, and formal classification. The emphasis today is on the nature of species, the origin of species, and the relation of species to their environment.

Twelve long years have passed by since the last International Ornithological Congress, long years in more than one sense. But in spite of all the misery and destruction which the past unholy war has brought upon the world, it has not reduced scientific productivity to a very marked extent. More than 18 000 ornithological papers have been published since the Rouen Congress and nearly 200 of them touch upon the problem of speciation. Only a cursory survey of this vast literature can be attempted in the forty-five minutes allotted to me. Fuller details can be found also in a number of recent summaries that were published in book form (Mayr, 1942; Huxley, 1942; Lack, 1947a). The genetic basis of speciation and other more general aspects of evolution have been discussed in other volumes (Dobzhansky, 1941; Bauer and Timoféeff-Ressovsky, 1943; Simpson, 1944; Rensch, 1947; Jepsen, Simpson, and Mayr, 1949). My own discussion will concentrate on the controversial issues and unsolved problems. We ornithologists can be proud of our contributions to this field. The present biological concept of the species, as well as the theory of geographical speciation, was to a large extent developed by ornithologists on the basis of ornithological material.

No rational theory of the origin of species was possible until the concepts of the nature and structure of species had matured. Let us therefore say a few words on these two topics.

*The nature of species.* The biologist of today considers species to have the following essential characteristics: A species is an aggregate of interbreeding natural populations which are not only reproductively isolated from other such aggregates but also ecologically specialized sufficiently so as not to compete with other such species. The problem of the origin of species then resolves itself in the question: How can *one* group of interbreeding populations break up into two or more which are not only reproductively isolated from each other but also ecologically compatible?

A study of the population *structure of species* has yielded the clues for the solution of this problem. As stated, species are usually polytypic, that is, they are composed of lesser units, subspecies and local populations, which deviate more or less from each other. Furthermore, through their geographical extension species are multidimensional systems. Species, as understood by us today, are a far cry from the necessarily monotypic, typological species of Linnaeus and his contemporaries.

The study of the structure of species is the chief occupation of the bird taxonomist of today. It is impossible to refer to more than merely a fraction of the recently published monographic studies on the geographical variation of species (Aldrich, 1943, 1946b; Behle, 1942; Bond, 1943; Chapin, 1948, 1949; Chapman, 1940; Dunajewski, 1939; Hawbecker, 1948; Jany, 1948; Johansen, 1945, 1946, 1947; Lack, 1945, 1947a, 1947b; Mayr, 1941, 1942a, 1949a, 1949b, 1949c, 1950b; Mayr and Amadon, 1947; Mayr and Moynihan, 1946; Miller 1941; Moreau, 1948b; Pateff, 1947; Pitelka, 1945a; Ripley and Birckhead, 1942; Ripley, 1941; Salomonsen, 1944; Snyder and Shortt, 1946; Stresemann, 1940; Vaurie, 1949a, 1949b; Voous, 1947, 1949; Voous and Van Marle, 1949). All these studies show that most species of birds are polytypic, that is, they are composed of several subspecies. In New Guinea, for instance, 80 per cent of all species are polytypic (Mayr, 1942) and among temperate zone birds about 60–80 per cent. Accurate comparative studies on the percentage of monotypic species in various parts of the world have not yet been made. They can be undertaken only where reliable faunal lists are available.

## Subspecies

Though not strictly part of our subject, I would like to say a few words about *subspecies*. Unlike the effective local population (Sewall Wright) or the species, which can be defined biologically, the subspecies is primarily a taxonomic concept. It is a population or aggregate of populations which differs taxonomically from other such aggregates within a species. A subspecies cannot clearly be delimited from local populations on one hand and species on the other. In the past, certain authors have tried to name every population that differs in average characters. That this policy is nonsense has been made clear by the population geneticists who have shown that no two populations of sexually reproducing animals are exactly alike in the frequencies of polymorph genes and the means of multifactorial characters. To be recognized as different subspecies it is therefore not sufficient that two populations merely differ; they must differ "taxonomically." The standard of this "taxonomic" difference, in the opinion of some leading contemporary ornithologists, is best expressed by the so-called "75 per cent rule." A population can be recognized as a valid subspecies if 75 per cent of it differs from 100 per cent of the population with which it is compared. Amadon (1949) shows how this is best calculated from the available sample. In view of the slanting of the population curve a difference of 75 per cent from 98 per cent would seem to express current standards more accurately than the standard proposed by Amadon. The various standards were discussed by Rand and Traylor (1950).

The difference must be a "taxonomic" one, that is, it must be recognizable in museum specimens. It is important to emphasize this in view of the many slight differences among intrasubspecific populations and the physiological differences between populations and geographical races. In the White-crowned Sparrow (*Zonotrichia leucophrys*) the resident subspecies *nuttali* of the San Francisco Bay region differs in many ways from the migratory *pugetensis* (southern British Columbia to northern California). This includes differences in regard to beginning and length of breeding season, development of gonads and endocrine glands, song, and morphology (Blanchard, 1941). There is a broad transition zone, and some populations in northern California, though morphologically like *pugetensis*, are sedentary like *nuttali*. A similar physiological difference exists between the British and continental populations of the Starling (*Sturnus vulgaris*) (Bullough, 1942), but since there is no taxonomic difference, it is not admissible to recognize a separate subspecies for the British Starling (Thomson, 1943). Populations that differ with respect to migratory behavior and the physiology of the breeding cycle occur in many widespread subspecies of the temperate zone. It would lead to chaos to recognize all these population differences taxonomically.

Even so, bird taxonomy is loaded down with subspecies, which often obscure rather than clarify trends of geographical variation. On continents most subspecies intergrade with each other rather imperceptibly and also show a good deal of intrasubspecific variability (Behle, 1942; Lack, 1946). If there are reversals of the trends of variation, far distant populations may be indistinguishable and will have to bear the same subspecific name. There are many situations which provoke the feeling that trinomials have outlived their usefulness (Lack, 1947b).

Instead of expending their energy on the describing and naming of trifling subspecies, bird taxonomists might well devote more attention to the evaluation of trends in variation. Three basic rules are now quite evident, but require more quantitative documentation:

(1) Much geographical variation, particularly on continents, is clinal. These character clines are correlated with gradients in the selective factors of the environment.

(2) Peripheral or otherwise isolated subspecies of a species are the most distinct (Mayr and Vaurie, 1948).

(3) All taxonomic characters are in the last analysis controlled by selective factors of the physical and biotic environment.

More on (1) and (3) will be said in the next section.

The often striking divergence of peripheral subspecies or semispecies has been commented upon by many recent authors. Instances are *Junco vulcani* (Miller, 1941), *Ptilinopus huttoni* (Ripley and Birckhead, 1942), *Ducula galeata* (Mayr, 1942a), *Dicrurus megarhynchus* and four other groups of drongos (Mayr and Vaurie, 1948), *Dicaeum tristrami* (Mayr and Amadon, 1947), *Erithacus rubecula hyrcanus* and *superbus* (Lack, 1946), and many others. In fact, there is hardly a group of polytypic species which does not have some illustrations of this rule. Many of these peripheral populations are in the twilight zone between subspecies and species, and they are particularly important to the student of speciation as indicating the course of species formation.

## The Process of Speciation

The fact that species are not amorphous-homogeneous but that instead they have a definite structure consisting of populations and subspecies greatly facilitates the understanding of speciation. But, what do we mean by speciation? The term has been used in two different meanings. First it has been used to indicate a transformation in time, the phyletic evolution of the paleontologist. With his scanty fossil material, the ornithologist cannot make much of a contribution to this problem, although a promising beginning has been made for the Pleistocene of California (Howard, 1947a, 1947b; Fisher, 1947). When speaking of speciation, the neozoologist usually means the multiplication of species in space rather than their transformation in time. Excellent progress in this field has been made in recent years, in fact, the problem can be considered as solved in its major outlines. Many details remain to be filled in. The solution was the result of a painstaking analysis of many species, genera, and families of birds, such as those by Rensch of the birds of the Lesser Sunda Islands, Miller of Junco, Mayr of South Sea birds, Lack of the Galapagos Finches, and others quoted above. It is most gratifying to state that these authors are in almost complete agreement as to their results. These studies will therefore be summarized as a whole.

Speciation, in the sense of multiplication of species, proceeds in two steps. During the first step, a population (or subspecies or subspecies group) becomes isolated by extrinsic barriers. Gene interchange with the parental population is completely or almost completely interrupted. During this period of separation the isolated population becomes genetically reconstructed. If this change of the genetic makeup includes factors for reproductive isolation (isolating mechanisms), as well as for ecological compatibility, the isolated population may reach species level and can re-invade the range of the parental population. This process is called geographic speciation since geographical isolation (by barriers or by distance) seems to be needed to permit the genetic reorganization (Mayr, 1947).

Both the ecological compatibility as well as the reproductive isolation are controlled by hundreds of genes, and we can express the genetical difference between two sympatric (co-existing in the same geographical area) species as follows:

$$GD_{\text{A-B}} = IM_n + IM_p + IM_s + EC_n + EC_p + EC_s.$$

These letters mean:

$GD_{\text{A-B}}$ = Genetic difference between species A and B
$IM$ = Isolating mechanisms
$EC$ = Ecological compatibility factors
$n$ = Neutral
$p$ = Preadapted
$s$ = Acquired by selection

This formula means that the genetic differences between two species are composed of three sets of factors: those that are neutral with respect to isolating mechanisms ($IM_n$) and ecological compatibility ($EC_n$); those which the species acquired during their geographical isolation and which preadapted them for a subsequent overlap of the ranges ($IM_p$ and $EC_p$); and finally those differences which were favored by selection after the species had become sympatric ($IM_s$ and $EC_s$). It is logical (1) that no overlap between two species can occur unless $IM_p$ and $EC_p$ have been acquired during isolation, and (2) that there will be a high selective premium on the acquisition of factors that improve reproductive isolation and minimize ecological competition. Hence, there will be a continued accumulation of such factors ($IM_s$ and $EC_s$). The role of selection before and after the establishment of overlap was discussed by Mayr (1949d).

## The Proof for Geographical Speciation

The course of speciation through population divergence, as established by the taxonomist, is a vastly different concept of speciation than that held by the early Mendelians (De Vries, Bateson), who believed in instantaneous speciation by major mutations. Modern geneticists are nearly unanimous in endorsing the speciation concept of the naturalists, although there are still a few dissenters (e.g. Goldschmidt). A second line of attack on the concept of geographic speciation came from the proponents of sympatric speciation (see Thorpe, 1945 vs. Mayr, 1947). In view of these criticisms it may not be out of place to summarize once more the proofs for geographic speciation.

### *Geographic variation of species characters*

If isolating mechanisms ($IM_p$) and ecological compatibility ($EC_p$) evolve during geographical isolation, as postulated by the theory of geographical speciation, then one should find intermediate stages. Particularly one should find that isolating mechanisms, as well as ecological characteristics, are geographically variable. This is indeed the case. Owing to technical difficulties of keeping birds there is not as much proof for the geographical variability of isolating mechanisms in birds as in insects, mice, or fish. Fertility between geographical races seems to be occasionally reduced. Song in birds is an important component of the ethological isolating complex. Many cases of geographical variation of song have been described in the literature. Benson (1948) found it in thirty-three among 209 widespread species or groups of allopatric species (i. e. species with the geographical ranges not overlapping) of African birds. No voice difference was detected by him among thirteen pairs of sympatric species. I know of no pair of European, North American, or Papuan birds with identical songs or call notes. Perhaps Benson sets a higher standard for "difference." All sixteen species of birds that occur both in Britain and Teneriffe, Canary Islands, differ in their voices. In four species the song was strikingly different (Lack and Southern, 1949). The cases of circular overlap (see below) are good indirect proof for the geographical variation of isolating mechanisms.

### *Borderline cases*

There are many bird populations that are on the border between the subspecies and species level. No less than 94 of the 755 species of North American birds listed in the last A.O.U. Checklist are considered subspecies by some authors (Mayr, 1942). Twenty-five forms of Anatidae, considered subspecies by Delacour and Mayr (1945), are treated as species by other authors. Many of the examples of pseudo-conspecificity, listed below (Appendix), are also such borderline cases.

Some of these cases have received special attention in recent years. Among the African love birds (*Agapornis*) none of the eight forms widely overlaps the range of any other. The ranges of two forms, *fischeri* and *personata*, approach each other within twenty miles without signs of intergradation in spite of ecological similarity (Moreau, 1948 b). The woodpecker *Dendrocopos leucopterus* coexists geographically with *D. major* at various localities in central Asia, but it always inhabits broad-leaved trees (mostly poplars) in the lowlands, while *major* occurs at higher altitudes in coniferous forests. Some authors treat these forms as conspecific, others as separate species (Voous, 1947). A somewhat similar situation occurs in the *bokharensis* group of *Parus major* (Vaurie, 1950a).

The geese with their singular population structure are rich in borderline cases. The bean geese (*Anser fabalis*) include a southern group of large, long-billed subspecies in the taiga and a northern group of small short-billed subspecies in the tundra. (Johansen, 1945). In the Canada Geese (*Branta canadensis* group) it occasionally happens that neighboring nesting colonies differ in body size, voice (honking vs. cackling), nesting site (seacoast vs. inland), nest (mound vs. scrape), migration season, and other features. Intergradation between adjacent colonies may be entirely lacking and the temptation is great to assign these populations to two or three different species (e.g. Aldrich, 1946b). Yet, it has been impossible to arrange the subspecies satisfactorily into species. In fact, Bailey (1948) shows almost conclusively that *leucopareia* and *parvipes* form a perfect link between the small cackling geese on one side and the large honkers on the other. By secondary range expansion, however, large and small subspecies have come into secondary contact at various places without interbreeding. Thus, we have here another interesting borderline case between subspecies and species. Others occur in the *Rhipidura rufifrons* group (Mayr and Moynihan, 1946) and in *Pyrrhula* (Voous, 1949).

### *Circular overlaps*

The ideal proof for geographical speciation is presented by the cases of "circular overlap." The end links of a continuous chain of interbreeding subspecies overlap in such a case without interbreeding. Some examples were cited by Mayr (1942). Others have been described more recently. According to Johansen (1947) the chiff-chaff (*Phylloscopus collybita*) is another such case with the Caucasus being the area of overlap. There the northwestern *abietinus* occurs in the forests of the lower slopes while the southeastern *lorenzii* (of the *neglectus* group) is restricted to the sub-alpine forest zone.

Recent work indicates that in the most celebrated case of overlap matters are not as simple as once believed. I refer to the Herring Gull (*argentatus*)—Lesser Black-backed Gull (*fuscus*) overlap in Europe. This group is not composed of clinally intergrading populations, but rather of groups of subspecies which in certain zones of contact show no signs of intergradation and are ecologically segregated (Stresemann, 1943a). These gulls were apparently divided during the Pleistocene into a number of isolated populations which reached various levels of reproductive isolation and ecological compatibility (Stresemann and Timoféeff-Ressovsky, 1947). A similar situation exists in the American Herring Gulls, where *kumlieni* and *smithsonianus* overlap in northern Labrador and southern Baffin Land without interbreeding (Rand, 1943). The relation of these two forms to *thayeri* remains to be cleared up.

## Recently Completed Speciation

Recently completed speciation is indicated by three types of phenomena: (a) double invasions, (b) superspecies, and (c) marginal overlaps. The geographic basis of these three phenomena is apparent and they can be cited as proof for geographic speciation.

(a) Double invasions. If an island is repeatedly invaded by colonists from a distant mainland, it may happen that the descendants of the first wave of colonists have changed so much that they are reproductively isolated from the new arrivals. Stresemann was the first to recognize the importance of this phenomenon and Mayr (1942) listed many cases. Others have since been described: *Phaeornis* and *Loxops* on Kauai (Amadon, 1947); *Dicrurus* on Celebes and the Andamans (Vaurie, 1949a); *Pernis* in the Philippines (Stresemann, 1940); *Cinnyris jugularis* and *solaris* on Sumbawa and Flores (Mayr, 1944); *Philemon moluccensis* in Australia (Mayr, 1944); and six cases of completed double invasions in Ceylon and south India (Ripley, 1949).

(b) Superspecies. A monophyletic group of closely related allopatric species may be called a superspecies (Mayr, 1942). Superspecies are exceedingly common in island regions. They are 17 superspecies among 130 species of Solomon Islands birds. There are at least 11 superspecies (with 26 species) among the 145 species of Anatidae (Delacour and Mayr, 1945). Superspecies are found in the *Vini palmarum* and *V. peruviana* group, in *Ptilinopus luteovirens*, in *Ducula pacifica* and *Ducula latrans* (Amadon, 1943). They are common in the Celebes region: *Cyornis hoevelli* and *sanfordi*, *Eudynamis scolopacea* and *melanorhyncha*, *Hypothymis azurea* and *puella* (Stresemann, 1939), and in the Moluccas (*Gerygone fusca* group, *Oriolus*, *Sphecotheres*, *Philemon*, *Macropygia*) (Mayr, 1944). *Dicrurus hottentottus* and *D. adsimilis* belong to widespread superspecies (Vaurie, 1949a) and so does *Halcyon chloris* (Mayr, 1949c). Superspecies occur also in the *Dicaeidae* (Mayr and Amadon, 1947) and in *Agapornis* (Moreau, 1948b).

In all these cases the differences between allopatric forms are so striking that they appear to have reached species level during geographical isolation.

(c) Marginal overlaps. Occasionally one of the species of a superspecies expands into the range of another member of the superspecies with the result that there will be a smaller or greater overlap along the margins of their respective ranges. Several such cases were described by Mayr (1942); others are listed below in the list of pseudo-conspecific species pairs (Appendix). They occur in the *Treron curvirostra* group, in the *Anthreptes malaccensis* group, and in *Geokichla* (Mayr, 1944), in the *Rhipidura rufifrons* group (Mayr and Moynihan, 1946), in the *Ptilinopus purpuratus* group (Ripley and Birckhead, 1942), in *Anaimos* and *Dicaeum* (Mayr and Amadon, 1947), in fact in most actively speciating genera. Ripley (1945) has proposed the term interspecies for such ex-superspecies, but Moreau (1948a) considers this term superfluous. They have often been referred to simply as species groups.

The final step in this speciation process is the production of groups of full species that are more or less extensively sympatric. That they originated by geographical speciation is most evident in the case of species flocks that evolved on archipelagos. This has been worked out brilliantly by Lack (1947a) for the finches of the Galapagos Islands and by Amadon (1950) for the Drepaniidae of the Hawaiian Islands. On islands that are on or at the edge of continental shelves differentiation may not rise above the subspecies level, as is characteristic for most of the forms on the west Sumatran Islands (Ripley, 1944). This is due to the recency and insufficient isolation of these islands.

## Speciation on Continents

That speciation proceeds via geographical isolation is now universally admitted for insular species. At first sight, however, this explanation appears to meet difficulties when applied to continental species flocks. Genera rich in widespread species, such as *Parus* and *Sylvia* in Europe, *Emberiza* and *Carpodacus* in Asia, *Ploceus* in Africa, and *Dendroica* in America seem to defy the concept of geographic speciation. Closer analysis indicates, however, that speciation on continents obeys the same rules as on islands. The extrinsic isolating barriers in this case are not water gaps, but stretches of terrain that are uninhabitable because of ecological unsuitability. The best proof for this process of speciation is given by the many instances of incipient speciation in continental birds. These cases have frequently been obscured in the past by the bad habit of taxonomists to treat slightly and strikingly different subspecies alike, and either not to indicate subspecies groups at all or to raise them to species level.

The subspecies group indicates an important level of speciation as was pointed out by Stresemann (1940, Ornith. Monatsb., 48: 103–104) for the Jay (*Garrulus glandarius*). Well-defined subspecies groups occur in many species of the northern hemisphere. It can usually be shown that the Pleistocene glaciation was responsible for the development of these intraspecific groups. When the species were pushed southward they had to retreat into wooded refuges separated by cold steppes. This concept was first applied to European birds by Stresemann, but Rand (1948) has shown that it applies to North American birds equally well. Voous traces the history of subspecies groups in *Dendrocopos* (1947) and *Pyrrhula* (1949) with the help of this concept. Among the brown-eyed Juncos (*Junco*) of North America, the four continental subspecies groups also seem to fit the picture of refuges: *hyemalis* (Appalachians), *aikeni* (Black Hills), *caniceps* (Rocky Mountains), and *oreganus* (coast ranges). The three subspecies groups of the Ruffed Grouse (*Bonasa umbellus*), distinguished by Snyder and Shortt (1946), seem to have become differentiated in the Appalachians, Rocky Mountains, and coast range refuges. It would no doubt yield interesting results if somebody would systematically test all species pairs and subspecies groups in North America for possible origin in these Pleistocene refuges.

Speciation is incomplete in nearly all the mentioned cases and they do not, therefore, completely elucidate the problem of continental speciation. The isolated populations have often diverged so far morphologically that the subspecies groups are considered as species by some authors as, for instance, the four groups of brown-eyed Juncos by Miller (1941). Still they have apparently not reached either complete reproductive isolation or ecological compatibility. The period of isolation was apparently not long enough to permit the perfection of isolating mechanisms and the rapid post-Pleistocene northward movement of the vegetation has favored a mixing-up of the previously isolated populations.

A better example of the amount of isolation that may permit the completion of speciation is perhaps given by tropical forest birds that live in isolated patches of forest (particularly in the mountains). Numerous examples of this occur in Africa (although never properly tabulated and evaluated) and on the tabletop mountains near the Brazilian-Venezuelan frontier as shown by the splendid explorations of the Phelps, father and son.

Australia shows a different manifestation of the same process. This island continent has an arid interior surrounded by a more humid marginal zone. This humid belt is broad in humid periods, but contracts into a few coastal pockets at the height of an arid cycle. These pockets serve then as refuges (Gentilli, 1949) for the humidity-loving fauna and flora, and distinct populations evolve in each refuge. In the case of *Neositta*, the populations isolated during the last aridity cycle have not yet reached species level (Mayr, 1950). Pseudo-conspecific pairs of largely allopatric species also demonstrate geographic speciation on continents (Appendix).

## Allopatric Hybridization as Evidence of Incomplete Speciation

According to the theory of geographic speciation isolating mechanisms and ecological compatibility evolve during the geographical isolation of populations. It is to be expected that such geographical barriers sometimes break down before the speciation process is completed. Two things may happen in such a case. Either ecological compatibility has not yet developed, then we will get a peculiar mutual exclusion of the species ranges without interbreeding in the zone of contact. Such cases are listed in the Appendix. If, on the other hand, the isolating mechanisms have not yet evolved, hybridization will take place. There is little agreement in the literature on how to define hybridization. The term was coined to describe a relationship of individuals and difficulties are caused by extending it to populations. Hybridization in nature can be classified into two categories: sympatric and allopatric hybridization. Under sympatric hybridization I understand the occasional interbreeding of two otherwise well-delimited sympatric species. There is no conceptual difficulty in regard to this type of hybridization.

The real difficulty concerns allopatric hybridization, the interbreeding of allopatric populations in their zone of contact. If the two temporarily isolated populations diverged only very slightly we are loath to call such interbreeding hybridization, we call it intergradation. I have referred to it as secondary intergradation (Mayr, 1942) to distinguish it from the intergradation of populations that have always been in continuous contact and owe their difference to opposing selection pressures. All secondary intergradation indicates incomplete reproductive isolation. Such cases are extremely common, they probably occur in every but the most localized species. Miller (1941) has shown for *Junco* how many races "hybridize" in zones of contact, and Pateff (1947) has pointed out how many names have been given to hybrid populations in *Sturnus vulgaris.* Occasionally even strikingly different forms hybridize in a zone of contact as Meise has shown (Mayr, 1942). Such a case in northern Persia was described by Paludan (1940) and illustrated in a beautiful color plate. It involves two buntings of the genus *Emberiza* (*icterica* and *melanocephala*) which seem to interbreed indiscriminately in a narrow hybrid zone within which all individuals show signs of hybridism. This recalls a color plate by Sutton (1938) depicting a similar hybridization in American orioles. Those who accept a species definition based on reproductive isolation will call such freely interbreeding forms subspecies.

Incomplete speciation in southeastern Asia is indicated by the striking difference of subspecies in *Lanius schach* (Dunajewski, 1939) and *Microscelis madagascariensis* (Mayr, 1941).

Hybrid populations are normally characterized by pronounced variability but hybrid populations may become stabilized and the variability may drop to the "normal" level. Miller (1941) has shown this for *Junco cismontanus.* Whether or not *Pardalotus ornatus* is a species that owes its origin to a stabilized hybrid population is not certain (Hindwood and Mayr, 1946).

There is one specially interesting class of hybridizations which does not fit into the above categories. A most instructive case of it was described by Chapin (1948) for the African species of the flycatcher genus *Terpsiphone.* Here, certain species are essentially allopatric because habitat differences keep them segregated. Two species, *rufocinerea* and *rufiventer*, live in the rain forest of equatorial Africa, a third (*viridis*) in second growth and in wooded savannas. There are three areas in Africa (northwest Angola, Port. Guinea, and Uganda) where hybrid flocks have developed and individuals of the parental species are either present or absent. Chapin not only unmasked the polymorphism in these regions as hybridism but also provided an explanation. He showed that ecological conditions are responsible for it. Hybridism in *Terpsiphone* occurs where through the destruction of the rain forest by man (white or native) the forest and the savanna species are brought into exceptionally close contact. The hybridization between *Passer domesticus* and *P. hispaniolensis* also has an ecological explanation. It occurs where the Willow Sparrow has shifted from river bottom into human settlements. Ecological isolation is in birds as in the lower animals the isolating mechanism that is most easily broken down.

## Rate of Speciation

Numerous attempts have been made in recent years to fix the exact date at which a certain subspecies or species originated. Students of mammals base such calculations on an analysis of the known age of fossils. The avian record is rarely substantial enough to permit this method. The fossil Golden Eagles (*Aquila chrysaëtos*) from the Pleistocene of Rancho la Brea (California) differ from the living ones by a relatively low, flat, and broad skull with a heavy, broad beak and strong jaw. This fossil subspecies, which intergrades completely with modern Golden Eagles, is evidently ancestral to the modern form (Howard, 1947a). The exact dating of the tar pit remains has unfortunately not been possible. Presumably they are between 50 000 and 200 000 years old. The change in the California Condor (*Gymnogyps californianus*) from the Pleistocene to the recent subspecies was analyzed by Fisher (1947). There has been a very pronounced faunal change since the Pleistocene, for 33–49 per cent of the individuals among the fossils in the tar pits of Rancho la Brea belong to extinct species (Miller, 1940).

Since an adequate fossil record is available only for a few large-sized birds, calculations on the rate of speciation are usually based on indirect evidence, such as distributional data and amount of geographical variation. For instance, if a bird population is uniform in the wide area from eastern Siberia to northern Europe, the assumption is made that it has spread through this range post-glacially. This is assumed, for instance, by Voous (1947) for *Perisoreus, Dryocopus,* and *Dendrocopos leucotos*. Although there is much validity in such reasoning, rates of speciation and dispersal depend on many cryptic factors that are often overlooked. For instance, Zeuner (1943) tries to reconstruct the history of the *Troides* (*Ornithoptera*) section of the butterfly genus *Papilio* in the Malay Archipelago by correlating the ranges of the species and subspecies with the shifts of sea level in the wake of the various Pleistocene glaciatons. In order to simplify the picture, he has to make the assumption that evolution is equally rapid on small and on large islands, and also that there is no transoceanic dispersal. Since it is evident that neither of these assumptions is valid, the analysis loses most of its value. The non-biologist is apt to forget that species are not all alike. Each has its own particular evolutionary behavior. Not only are the inherent rates of evolution different in every species but also the physical and biological factors of the environment and their changes, degree of isolation, and size of population. The North American species that were split into separate populations in the various glacial refuges reached very different levels of speciation (Rand, 1948). Most water and shore birds reached species level (*Gavia immer* and *adamsi; Calidris semipalmata* and *maurii; Limnodromus griseus* and *scolopaceus; Nyroca affinis* and *marila;* and perhaps also *Branta bernicla* and *nigricans* and *Somateria mollissima* and *v-nigra*). A similar separation in many birds of the forest belt, such as in the genera *Parus, Canachites, Dendroica, Junco, Perisoreus, Sphyrapicus,* and *Zonotrichia,* has in most cases not led to completed speciation.

The geological data on which most of the dating is based are very insecure. Some geologists, for instance, state that the Hawaiian Islands originated in the Pliocene (Amadon, 1947). This would allow only an unbelievably short time for the evolution of the bizarre animal and plant life of these islands. As a matter of fact, the Hawaiian Islands are the tops of a chain of volcanic pinnacles rising from the ocean bottom. What the geologist can see is only the uppermost "skin" that covers up the earlier geological history. If the ocean bottom has dropped in the Hawaiian region as much as it has near Bikini (Mayr, 1951), it is quite possible that the history of these islands reaches back to the Mesozoic.

The exact dates of the recent pluvial and arid periods in the tropics are equally uncertain. Zoogeographers (Gentilli, 1949; Mayr, 1950) and geologists agree that there must have been a period of extreme drought in the recent past of Australia, but the geologists wonder whether it was as recently as 6 000 years ago or as early as 150 000 years ago. The avian data suggest that an earlier date (at least 50 000 years) is more likely.

The history of the last million years has been exceedingly complex. There were four or five glaciations with long interglacials; there were wet and dry cycles in the unglaciated areas as far south as the tropics; there were extensive shifts of sea level on all continental shelves; and in connection with this there were extensive shifts of the vegetational belts. It is not surprising therefore that students of speciation disagree occasionally on the dating of certain speciation events. Stresemann established the thesis, in a series of papers in 1919 and 1920, that the Scandinavian and Alpine ice caps had separated the eastern and western populations of many European bird species and thus caused subspeciation or speciation. As examples of subspeciation he listed the eastern and western races of *Sitta europaea, Aegithalos caudatus, Pyrrhula pyrrhula,* and *Corvus corone,* as cases of speciation the two creepers *Certhia familiaris* and *brachydactyla.* Salomonsen later extended this list to include quite a few western Palearctic species pairs. Steinbacher (1943, 1948) denies the idea of two European forest refuges and believes in a post-Pleistocene origin of the differences between west and east European subspecies. He makes the assumption that the forest belt was continuous south of the Alps and that there were no essential climatic differences between eastern and western Europe. The cited evidence for these assertions is not convincing. For instance, the fact that some loess occurs in northern France does not in the least prove that the climate in the western European forest belt near the Atlantic was the same as, let us say, in the Balkans or in Asia Minor. Also, there is no evidence for the complete continuity of the forest belt in the region south of the Alps. Stresemann's thesis of the origin of the more pronounced subspecies pairs during the Pleistocene still seems valid.

As far as the species pairs of forest birds are concerned that were listed by Salomonsen (including *Certhia familiaris* and *brachydactyla*), it seems probable that they originated in drought refuges either during interglacials or during the late Pliocene.

On the basis of the available knowledge it thus may seem very difficult to arrive at an exact timing of the speciation process. This is an over-pessimistic attitude. A few accurate timings are available, as for instance, for the age of the races of larks in the Nile delta (Moreau). It is also possible for the populations and subspecies that live on the Anamba and Natuna Islands and other small islands on the Sunda Shelf (Stresemann, 1939; Mayr and Vaurie, 1948). These populations became separated from those of the adjacent mainlands only when the Sunda Shelf was drowned at the end of the Pleistocene and are therefore less than 20 000, perhaps even less than 10 000 years old.

Claims have been made repeatedly for rapid recent changes in the genetic composition of polymorph populations of birds. The occurrence of such changes is highly probable in view of similar changes in insect populations, both free-living and in laboratories. However, for birds it is not well substantiated. It has been questioned by Mayr (1942) for *Rhipidura fuliginosa* and *Coereba flaveola* and has been refuted by Benson (1946) for *Lybius zombae*. There is some evidence for a rapid increase of the Blue Goose (*Anser coerulescens*) at the cost of the Lesser Snow Goose ("*hyberboreus*"), but it is not certain how far this has been due to a relaxation of hunting pressure.

## Factors of Speciation

The factors that cause and guide speciation have been discussed in a number of recent books (Mayr, 1942; Huxley, 1942) so that it is unnecessary to discuss them in detail.

As far as the genetic factors are concerned, it is now realized that species differ by very many genes, certainly hundreds, perhaps even thousands. This has been established for animals other than birds since birds are particularly unsuitable for genetic research. The few thorough genetic examinations of birds are, however, fully consistent with this hypothesis. For instance, merely the genes that control the antigenic characters of the red blood cells of three species of *Streptopelia* are situated on no less than nine or ten chromosomes and the evidence indicates the presence of multiple characters on several of these chromosomes (see Irwin, 1949, for the latest summary of the work of Irwin and his associates). Those interested in a more complete discussion of the genetic aspects of speciation should consult Dobzhansky (1941), Bauer and Timoféeff-Ressovsky (1943), or Jepsen, Simpson, and Mayr (1949).

The deflation of the role of single mutations goes even further. The De Vriesian mutation concept became the basis of Cuénot's preadaptation principle. According to this typological concept the sudden emergence of new genetic types forces them into new niches for which they are preadapted. Modern genetics, thinking in terms of populations, make the unlikeliness of this process apparent. In fact, with a good deal of justification, some authors now stress the importance of habit formation as a forerunner of genetic change. Once established through conditioning, such a habit favors the selection of facilitating structures. One might call this a process of genetic post-adaptation. In a population of falcons that has learned to feed on bats, there will be selection pressure in favor of individuals that have the best equipment for the job. As a result of this selection pressure, a gradual genetic modification of the population will take place (Cushing, 1944). In regard to epigamic structures (crests, plumes) the movement behavior precedes the development of the structure, as Lorenz has emphasized correctly. Conditioning alone, however, can never lead to the existence of two sympatric populations (Mayr, 1947).

Of more immediate interest to the naturalist than the genetic factors of speciation are the ecological ones. Since speciation is dependent on the genetic reconstruction of isolated populations, the nature of the isolating barriers is of primary importance. Gentilli (1949) has given a summary of such barriers. The effect of water gaps in the speciation of island birds is too obvious to require further discussion (Lack, 1947a). Ecologically unsuitable terrain is the usual barrier on continents. The role of ice and correlated vegetational changes for the speciation of North American birds is stressed by Rand (1948). Droughts which restrict the vegetation to small pockets or refuges are an important agent of speciation in arid countries as Australia (Gentilli, 1949; Mayr, 1950), India (Ripley, 1949), and Africa (Moreau, 1948b).

Equally important as the extrinsic barriers themselves are the intrinsic factors, such as habitat selection and homing that re-enforce them (Mayr, 1949a). Much attention is paid in population genetics to effective population size, dispersal, in short, to all the factors that contribute to the factor $m$ in Sewall Wright's formulae ($m$= rate of change in the genetic composition of a population due to immigration). Miller (1947) and Haartman (1949) have shown how different these factors are in different species and even in different parts of the range of the same species. We are only at the beginning of this important branch of ornithological research which is based on the banding and careful analysis of local bird populations. Dispersal facility may be very different in closely related species. *Zosterops rendovae* respects water gaps of only one and one-half miles in width while *Z. lateralis* crossed in 1856 the 1 200-mile wide gap between Australia and New Zealand. The eleven species and superspecies of drongos (Dicruridae) can be divided into four groups according to their dispersal faculties. Only two superspecies (*adsimilis* and *hottentottus*) are freely capable of colonizing oceanic islands. It is not surprising that these two superspecies have developed the greatest number of species and subspecies in the family (Mayr and Vaurie, 1948). The total size of a species population is also of evolutionary importance. Palmgren (1942) has calculated it for some of the forest-inhabiting species in southern Finland and Miller (1947) for some insular species.

## Speciation and Higher Categories

There are quite a few biologists, particularly paleontologists, who insist that the origin of higher categories is a process that differs basically from the origin of new species. That this opinion is wrong has been demonstrated conclusively in a number of recent works (Simpson, 1944; Rensch, 1947; Jepsen, Simpson, and Mayr, 1949) so that it is superfluous to go once more over the entire ground. However, the bird speciation literature has shed considerable light on the subject and some of this may be summarized here.

The first step in the origin of higher categories is the origin of new genera. If this could be explained, much would be gained toward an understanding of the origin of the still higher categories. No progress can be made in this until we know what a genus is. It is now evident that the genus cannot be defined objectively as can the species (Mayr, 1943). Most genera have been based, in the past, on "generic characters." If we study such characters as for instance the formerly accepted generic characters in the drongos (crest, shape of tail feathers), we find that they vary geographically (Mayr and Vaurie, 1948). The same is true for plumes in the birds of paradise (*Astrapia, Parotia, Diphyllodes*) and for the bill structure in the Dicaeidae (Mayr and Amadon, 1947). In all these cases, the so-called genera obviously originated by geographical variation, but it must be admitted that most of these genera are based on rather slender foundations. The so-called generic characters are in many of these cases epigamic characters of local populations of males.

During the past twenty years there has been a steady trend away from the narrow, purely morphologically defined genus. This movement has led not only toward a great simplification of nomenclature by reducing the number of genera from about 4 000 to about 1 500–1 700, it has also given the genus a new meaning, a biological one. The genus is now defined not merely as a group of related species but as a group of species with similar ecology. When a species shifts into a major new ecological niche, the stage is set for the origin of a new genus. I say major niche because even every species is, of course, in a different niche. Unfortunately it cannot be defined exactly what a major niche is, and this is the reason why genera cannot be delimited as accurately as species.

This process of the entering of new niches has been discussed by Lack (1947a) and by Miller (1949). It occurs most frequently and most rapidly where there are the greatest number of empty niches, namely on well isolated ancient islands. Examples of rapid adaptive radiation and hence the rapid origin of higher categories by geographic speciation are presented by the Geospizinae in the Galapagos Islands, by the Vangidae and Philepittidae of Madagascar, and especially by the Drepaniidae of Hawaii. A particularly instructive example in the genus *Hemignathus* has been analyzed in detail by Amadon (1947). This process of shifting into a new niche is also often evident in continental genera of birds. Miller (1949) shows how the thrashers (*Toxostoma*) evolved from mockingbird (*Mimus*)-like ancestors through a reconstruction of the bill (and other parts of the body) in correlation with a shift into a new niche, namely, a more terrestrial mode of life with digging as the major method of food getting.

The entering of new ecological niches can be followed step by step in these and many other cases and there is no need to postulate evolution by major saltations.

## Open Problems

Much has been learned about the process and the causes of speciation, but much still remains to be learned. No sooner has one problem been solved than several new ones become apparent. What then are the problems that lie ahead of us? It would lead too far to give a complete inventory, but I would like to single out three groups of problems that are of immediate interest. Work on them has already started actively.

### *Comparative systematics*

The first is the problem of comparative systematics. By this I mean the study of the differences in speciation patterns in different groups of birds, in birds of different regions, and in birds with different ecologies. Beginnings in this field have been made by Rensch, Mayr, and others, but no comprehensive analysis is as yet available. Nobody has yet studied differences in speciation patterns between predators and prey, between Passeres and non-Passeres, or compared insect-, nectar-, and seed-eating birds. In particular, the question should be studied whether or not there are inherent rates of speciation in different orders and families of birds. On the whole, one has the impression that genetic heritage is rather unimportant in the matter of subspecies and species formation as compared with such factors as population structure and dispersal facilities.

Rensch compared subspeciation in Palearctic birds and found that the number of subspecies per polytypic species was about twice as high in sedentary species as in migratory ones (Mayr, 1942). A similar analysis for North America and other parts of the world would be very desirable.

No correlation between size of species range and environmental factors has so far been worked out. However, water birds and other birds of large size usually have much larger ranges than the small song birds.

Topography is by far the most important element affecting species structure. In island regions many localized species or strikingly different subspecies occur; in continental regions most species are widespread with slight or no geographical variation. In the Solomon Islands, for instance, 52 per cent of the species are in the former category and only 24 per cent in the latter; in continental Manchuria only 3 per cent of the species are localized or with striking subspecies, while 69 per cent are widespread with slight or no geographic variation (Mayr, 1942).

Additional work in comparative systematics would permit us to state the relative importance of the various speciation factors more precisely.

### *Taxonomic characters*

The analysis of the significance of taxonomic characters has made significant progress in recent years. Not so many years ago it was believed that only the characters of genera and higher categories had adaptive value and that the characters of species and lower categories were without selective significance. It was thought that they were merely accidents of nature. More and more evidence is now accumulating to indicate that most, if not all, species and subspecies characters have positive selective values.

The first line evidence consists of the ecological rules. As Rensch and others have shown (Mayr, 1942) many taxonomic characters, such as size, proportion, relative size of extremities and other appendages, color, and others, vary geographically in a most regular manner, parallel to the determining factors of the environment. The work of Jany (1948) on the manifestations of Gloger's Rule in North African shrikes and of Lack (1947c) on the geographical variation of clutch size are among the more recent contributions to this field.

If the change of character is very regular, it may form a geographical gradient or *cline*, as Huxley has called it. Such clines have been frequently discussed in the recent ornithological literature, as for *Pyrrhula* by Voous (1949), for several species of *Dicrurus* by Mayr and Vaurie (1948), and for the white-breasted nuthatch (*Sitta carolinensis*) by Hawbecker (1948). Contrary to expectations the southernmost populations of this nuthatch have the largest measurements. The author did not investigate whether this unexpected trend was due to competition with a smaller species or due to geographical variation of favorite food or due to some other reason.

After we eliminate all taxonomic characters on whose variation the ecological rules are based, we are still left with a large residue of characters that are not under the obvious selective control of the environment. Let us take, for example, the differences between the North American warblers of the genus *Dendroica* or the titmice of the genus *Parus*. It has been suggested that these species characters are epigamic characters and may serve as isolating mechanisms between closely related species. Is this really their entire significance?

Unsurmountable difficulties may seem to prevent a solution of this problem. How should one determine whether or not a black cap or a pectoral band have selective values? Fortunately, some very convincing evidence has turned up as byproduct of the study of polymorphism. A short survey of this field would seem appropriate in view of its new significance.

*Polymorphism.* Polymorphism is the occurrence in the same population of two or more distinct forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation (after Ford).

An earlier summary of the occurrence of polymorphism in birds was presented by Stresemann (1926) and a later one by Mayr (1942). The polymorphism of many additional species has been studied in recent years as, for instance, in *Falco rusticolus* (Todd and Friedmann, 1947), *Anser coerulescens* (Manning, 1942), *Accipiter novaehollandiae* (Southern and Serventy, 1947), *Macronectes giganteus* (Serventy, 1943), *Uria aalge* (Southern and Reeve, 1942), *Stercorarius parasiticus* (Southern, 1943), *Macropygia mackinlayi* (Amadon, 1943), *Halcyon saurophaga* (Mayr, 1949c), *Cracticus quoyi* (Stresemann, 1943b), *Poëphila gouldiae* (Southern, 1946), *Oenanthe* (Vaurie, 1949b), and *Chlorophoneus* (Chapin, 1947).

The fact that there is geographical variation in the frequency of the alternative forms and that this frequency often changes in the form of a rather regular cline had long suggested that the alleles in polymorphic populations differ in selective values. On this basis, however, it was hard to understand how the balance between the alleles should be maintained at a given locality. This puzzle was solved by R. A. Fisher, who postulated a condition of balanced polymorphism due to a superiority of the heterozygotes over both classes of homozygotes. The frequency of the polymorph genes is then determined by the ratio of the viability of the homozygotes to each other and to the heterozygotes. This brilliant hypothesis has been substantiated in the meantime by experimental work (references in Mayr and Stresemann, 1950).

The selective value of the alleles should be different in different environments and this is indeed indicated by the fact that there is geographical variation of the frequency of the alleles in nearly all known cases of polymorphism. Presumably, there are also some shifts from year to year but the counts are rarely accurate enough to substantiate this possibility. In birds there is the case of the black mutant of the Rock Dove (*Columba livia*) of the Faeroe Islands which increases in years that are favorable for the species until it comprises about 14 per cent of the population. This same mutant is more vulnerable to severe conditions and decreases in frequency to about 5 per cent during a hard winter (Petersen and Williamson, 1949). Here it is clearly established that the black mutant is superior during favorable, warm periods, and the "wild type" during severe winters.

The bearing of this observation on the interpretation of subspecies and species characters is evident. Indeed, we find that in many polymorph species an allele has become fixed in parts of the range and has become *the* subspecies character as, for instance, in *Oenanthe* and *Cinclus* (Mayr and Stresemann, 1950). Such difficult taxonomic situations, as that found in *Motacilla flava*, are best interpreted on this basis, as was done correctly by Grote (1937). Although "pure" subspecies of this bird are known from many areas, it is true that exceedingly polymorph populations have been described from others. Gray-headed, yellow-headed, and black-headed birds breed together in such areas. To call each of these plumage types a different species is a simple, but biologically incorrect solution. Not only are there no differences except such of coloration, but all sorts of intermediate types have been found and there is much evidence for indiscriminate interbreeding. On the basis of the information presented by Johansen (1946) it appears that *Motacilla flava* includes several strikingly distinct subspecies groups and that instead of blending intergradation in the hybrid belts where they meet there is Mendelian segregation leading to polymorph populations.

*Adaptive characters.* Why a yellow-headed bird should be superior in one area and a gray-headed in another is not apparent. Still, we must never lose sight of the fact that it is not necessarily the taxonomic character that is adaptive but rather the underlying gene. This gene produces not only the visible phenotype but it also controls all sorts of invisible physiological processes which may have very pronounced selective properties. This seems to be true particularly for those pigmentation characters that follow Gloger's Rule. There is a definite correlation between the deposition of eumelanin and phaeomelanin in the feathers and humidity or temperature in the local climate (see Jany, 1948, and Frank, 1938, for special cases). Snyder and Shortt (1946) find that the Appalachian group of races of the Ruffed Grouse (*Bonasa umbellus*) are characterized by darkness and high amounts of phaeomelanin, while the Rocky Mountain group of the interior tends to paler and grayer coloration. They report a similar distribution of pigment characters in the Song Sparrow (*Melospiza melodia*), the House Wren (*Troglodytes aedon*), and the Horned Owl (*Bubo virginianus*). A systematic study of such distribution patterns of coloration is badly needed.

The phenotype may also have a direct adaptive value. The best known case is the cryptic coloration of desert birds, particularly larks. This was discussed exhaustively in the earlier literature, most recently by Hoesch and Niethammer (1940) and by Meinertzhagen (1950). In the American Horned Larks (*Eremophila alpestris*) there is in several races a fairly close correlation with soil color: reddish *rubea* lives on the red soils of Sacramento Valley, dark *merrilli* on the dark soils of northwestern California, and pallid *utahensis* on the whitish alkaline soils of the Great Salt Lake region (Behle, 1942).

Such cryptic coloration occurs not only as subspecies, but also as species character. Most desert birds have a sandy coloration and most birds of dry savannas are inconspicuously or disruptively colored. It is interesting that most of the ant-eating woodpeckers have barred upperparts, such as the flicker (*Colaptes*) and the ant-eating species in the genus *Dendrocopos* (*macei, atratus, analis*). Sitting on the ground, while feeding on ants, they are exposed to heavy predation, and this disruptive coloration is undoubtedly of considerable survival value.

There are some exceptions to this rule of the cryptic or disruptive coloration of birds of the open country which at first sight are very puzzling. For instance, many of the desert chats (*Oenanthe*) are of a conspicuous black and white color. Cott (1947) made the remarkable discovery that this conspicuousness is, in fact, a warning coloration! He found that the flesh of such conspicuously colored birds has a very disagreeable taste. Meinertzhagen (1950) confirmed that the taste of a conspicuously colored desert bustard (*Afrotis atra*) was "disgusting." Even though the final proof (avoidance by predators) is still wanting, it is highly probable that even here the taxonomic character (a color pattern) has adaptive value.

It is hardly necessary to mention at this point such conspicuously adaptive characters as the pointed wings of migratory and high altitude birds or the bill characters of the various races of the crossbill (*Loxia curvirostra*). The bill, in particular, is one of the most plastic characters in birds and a most sensitive indicator of ecological conditions. The amount of variation within a single polytypic species or superspecies is often striking enough to simulate generic difference (e.g. *Acrocephalus luscinia-syrinx* group, *Myiagra ferrocyanea, Dicrurus hottentottus*). The extreme plasticity of the bill in the Galapagos Finches was recently discussed by Lack (1947a), in the Drepaniidae by Amadon (1947), and in the flowerpeckers (Dicaeidae) by Mayr and Amadon (1947). The bill often responds with great sensitivity to temperature differences, as demanded by Allen's rule. To include a group of mountain species of *Coracina* into a single species group on account of their short bill, as was done by Voous and Van Marle (1949) (against Ripley, 1941), seems therefore ill advised. Mountain birds often have shorter bills than their lowland relatives.

## Character Geography and Faunal History

The recent comprehension of the adaptive importance of taxonomic characters warns to caution when using them for the reconstruction of faunal histories. Unfortunately, they cannot be dispensed with entirely, since we ornithologists lack a fossil record almost completely. Fortunately, they can be used if interpreted cautiously. This has not always been the case in recent studies (Chapman, 1940; Johansen, 1946; Mayr and Moynihan, 1946; Voous, 1947, 1949; Voous and Van Marle, 1949). Voous (1949), for instance, criticizes Görnitz quite rightly for considering *Pyrrhula cineracea* and *murina* as "relict" relatives, merely because they are superficially similar. But then he proceeds to reconstruct the history of the *Coracina striata* group on the basis of presence or abscence of barring. There is much in the distribution pattern of this species to suggest that this is an adaptive character and that isolated barred subspecies are not necessarily more closely related to each other than to unbarred forms.

It is possible, and indeed well documented, that a character may be gained and lost repeatedly in a chain of forms. Terminal forms, for instance, may acquire secondarily an aspect of primitiveness. The most isolated forms in some polytypic species or superspecies of Polynesian birds show this very well indeed, for instance, *Lalage sharpei* (Samoa) in the *Lalage maculosa* complex and *Todirhamphus venerata* in the *Halcyon chloris* complex. In *Pachycephala pectoralis* sexual dimorphism has been lost twice, on Rennell Island (*feminina*) and on Norfolk Island (*xanthoprocta*), giving these two subspecies a pseudo-primitive aspect. This potentiality of secondary primitiveness must be taken into consideration when reconstructing faunal histories. The genus *Junco*, for instance, has all the earmarks of an immigrant from the Old World (of the originally American Emberizinae!) (Mayr, 1942b). The Chiriqui Junco (*J. vulcani*) is therefore presumably not a primarily primitive form, but owes its primitive character to a secondary loss of characters in its specialized environment.

Students who devote their attention to the reconstruction of faunal histories with the help of a taxonomic character analysis have committed some obvious blunders by not clearly realizing the dangers of this technique. To prevent other investigators from falling into the same traps as their less fortunate predecessors, it may be useful to point out some of the most frequent fallacies.

*In regard to characters*

(a) that characters have no selective significance and that the occurrence of similar characters in widely separated areas must indicate former continuities.

(b) that all evolution is unidirectional, starting from a primitive stage and proceeding from there irresistibly to a specialized condition.

(c) that characters are inexorably correlated with each other so that if one character in a form is primitive, its other characters must also be primitive.

*In regard to distribution*

(a) that birds cannot cross barriers and that discontinuous distributions indicate a former continuity of habitat.

(b) that the habitat preference is unalterably constant through space or geological time.

*In regard to evolutionary change*

that there is a standard rate of evolutionary change in various species and subspecies and various characters.

It so happens that all of these statements are partly true, in fact, they are often true. But, they are not invariably true, indeed, the number of exceptions for many of these statements is very large. It is actually so large as to invalidate many of the conclusions reached in some recent zoogeographical-evolutionary essays. A little more caution in such studies would seem advisable, otherwise there is danger that this entire working method will fall in disrepute.

There is one group of characters that seems to vary independently of the environment, namely, the epigamic characters. The various plume and color characters, by which the allopatric species of *Astrapia* and *Parotia* on the mountains of New Guinea differ from each other, evolved to enhance the conspicuousness of the males during their display, rather than as a response to definite requirements of the local climate. This is, no doubt, true for most of the sexually dimorphic characters displayed in courtship.

But, even these characters have been selected (for maximum stimulatory value!).

It is very doubtful, then, whether there is any "random" variation of taxonomic characters. Rensch (1947), for instance, quotes the geographical variation of the colorful tropical lory *Trichoglossus haematodus* as an instance of random variation. However, Cain (MS) has shown that there are clines and other regularities in this variation and has established correlations between prevailing colors and the environment of the various subspecies. No definite evidence for randomness could be found.

### The Role of Ecological Factors

The realization that conspecific populations replace each other in space became the most productive concept in bird taxonomy. Every isolated bird species was suspected of being a disguised member of an allopatric species. The tremendous heuristic value of this method is well known. It permitted the reduction of the 19 000 species of Sharpe's *Handlist* to the 8 600 species of birds recognized at present (Mayr, 1946). However, beyond these purely practical results, it led to a new and deeper understanding of the nature of species and of the process of species formation. This period of taxonomic research was clearly dominated by the geographical approach; species were defined as complexes of geographical races and the new concept of speciation was called the theory of geographic speciation. Although this terminology is quite correct, it failed to bring out sufficiently the equally or even more important ecological aspects of species and speciation.

This neglect of the ecological factors is historically understandable since the role of the environment was almost consistently misinterpreted in the decades before 1940. Again and again attempts were made to explain the ecological differences between species as evidence for sympatric speciation, that is, for the origin of species through ecological specialization without geographical isolation. To counteract such views, it was necessary to stress the geographical aspects of speciation. When, by 1942, geographical speciation was universally accepted as the only mode of speciation in birds (Mayr, 1942) the time had come for a re-evaluation of the ecological factors.

This was done independently and simultaneously in Germany by Stresemann and in England by Lack. While Lack (1944 ff.) studied the effects of competition, Stresemann (1943 a) was primarily concerned with the evolutionary role of minor or major ecological differences among local populations. This may then be the starting point of our considerations.

### *Ecological characteristics of populations*

Although all the members of a species or at least of a subspecies agree in their essential ecological requirements, it must never be forgotten that there are differences not only among individuals but also among local populations. Every field ornithologist is familiar with such cases. The Savanna Sparrow (*Passerculus sandwichensis*) of the eastern United States is found in coastal salt marshes and also on dry uplands in the interior. The Redwing (*Agelaius phoeniceus*) normally lives in cattail (*Typha*) swamps, but breeding colonies have been found in alfalfa fields and even in young pine plantations. The Swainson's Warbler (*Limnothlypis swainsoni*) lives in the cane brakes of the coastal marshes in the southern United States but also in the southern Appalachian highlands above 3000 feet in thickets of rhododendron, mountain laurel, hemlock, and American holly. There are no connecting populations between the two "ecotypes" (Brooks, 1942). Similar cases have been described by Peitzmeier (1943) and others and partial reviews of the literature have been given by Stresemann (1943a) and by Mayr (1949a). There is no doubt that there is a great deal of ecological variation not only on the level of individual differences but also on the population level. What interests us primarily in this connection is the role which this ecological variability plays in the process of speciation.

There has been much discussion in the literature (Stresemann, 1943a; Timoféeff-Ressovsky, 1943; Cushing, 1941, 1944; Mayr, 1947) about whether or not these ecological differences have a genetic basis. Actually this is a rather sterile discussion, since it is evident that non-genetic conditioning as well as genetic differences are involved. But, the relation between ecological variability and speciation is not yet clearly understood. A species, which is so narrow in its requirements that it can survive anywhere only in the same narrow niche, will have a very limited range and little chance to break up into several species. The same is true, at the other extreme, for a species with high dispersal faculties that is ecologically so tolerant that it will prosper in every conceivable niche, as for instance, man. A species that has rather specific requirements at any one given locality but which is sufficiently plastic to be able to shift into a new niche when colonizing new geographical regions, has the best chance for speciation.

One of the important subjects of speciation research, then, is the mode by which species colonize new geographical areas. Though this is, strictly speaking, a subject of zoogeographical or ecological research, it has significant bearing on speciation. The most important results can be summarized in these statements: (1) new areas are normally settled by young birds that are either forced out of their birthplace by population pressure or whose homing faculty (or *Ortstreue*) is not perfectly developed, (2) the optimum biotopes (habitats) in the new district are occupied first and the inferior habitats are filled only gradually and with much delay, and (3) for every successful colonization there are many that are only temporarily successful or completely unsuccessful.

Peitzmeier (1942) is particularly impressed by the ecological conservativism of most species. When the mistle thrush (*Turdus viscivorus*) spread in recent years from northern France and Belgium into Holland and the lowlands of northwestern Germany, it occupied open deciduous woods and groves of trees near human habitations, the very habitats occupied in the area of origin of these populations of mistle thrushes. On the other hand, the mistle thrush populations of the coniferous woods of the hill country of northwestern Germany were apparently unable to change their habitat preference and invade the otherwise so favorable adjacent lowlands.

There has been one great clarification in our thoughts on this subject. Preadaptation, in the sense of Cuénot, does not exist. Cuénot, who was dominated by a typological species and subspecies concept and by a De Vriesian concept of macromutations, thought that the colonization of new territories was possible only if through mutation new "types" originated that were inferior in their home range, but preadapted for the new area. These preadapted individuals would then become in this area the progenitors of a new type.

Stresemann (1943a), Cushing (1944), Thorpe (1945), Gause (1947), and other recent authors emphasize a different process. They believe that most populations are started by individuals that are able to adjust themselves (non-genetically) to new conditions when colonizing new regions. Once such a population has become conditioned to a new niche, a new set of selective factors will operate to reconstruct this population genetically. This hypothesis is sound as long as it does not include the concept that two such ecologically slightly differing populations could co-exist sympatrically without reproductive isolating mechanisms. However, in all cases of explosive range expansion such as have occurred in the Serin Finch (*Serinus serinus*) and in the Ring Dove (*Streptopelia decaocto*), there is reason to believe that this expansion was initiated by a genetic alteration of the peripheral populations.

Some recent authors have advocated a dualistic speciation process, either via geographical races or via ecological races. It cannot be stressed too emphatically that there is no such dualism. There is no ecological race that is not spatially isolated and no geographical race that does not show certain ecological differences. The apparent discrepancy is most easily resolved if we think of these races as populations. Each of these populations has its own area of distribution—no matter how small—and is adapted to a specific niche within this area. It is the only population in this area and is therefore both geographical and ecological. The difficulties usually arise from the more or less arbitrary combining of such populations into the subspecies of the taxonomist.

An excellent study by Marshall (1948) of the ecological races of the Song Sparrow (*Melospiza melodia*) in the San Francisco Bay region of California illustrates the interdependence of geographical and ecological factors in an almost diagrammatic manner. Three subspecies occur here in salt water or brackish marshes and a fourth one near fresh water in the uplands. The upland subspecies is separated in most areas from the salt marsh subspecies by an ecologically unsuitable dry plain. Wherever this isolation exists there is a sharply defined taxonomic difference between upland and marsh birds while the marsh populations intergrade with each clinally. Where isolation is absent, the morphological difference between populations of different habitats is slight or absent: "Without this isolation the Tomales Bay salt marsh birds are identical in morphological attributes with the birds in fresh-water habitats surrounding them. Wherever it is lacking between bay marsh and upland populations as at Richardson Bay, Corte Madera and San Pablo, the respective populations become practically indistinguishable" (Marshall, l.c.). In a few places the marsh and upland birds have come into secondary contact and the area and amount of intergradation is governed entirely by the configuration of the habitat. At San Francisquito Creek, where two contrasting habitat types meet abruptly, there is little mixing of the neighboring subspecies, apparently due to habitat selection rather than to non-random mating. These ecological races of the Song Sparrow owe their origin and maintenance to a large degree to geographical isolation. They are not only ecological races, they are also geographical races.

### *Ecological characteristics of subspecies and species*

The differences in ecological requirements among individuals and local populations are usually believed to be of minor degree within the "typical" ecology of the species. This is indeed normally the case. However, in an unexpectedly great number of species there is striking geographical variability in ecological characters. Such instances have been listed by Brooks (1942), Stresemann (1943a), and Mayr (1942, 1949a). The Island Thrush (*Turdus poliocephalus*), for instance, feeds on Rennell Island near the sea-shore among coral boulders, while nearby on Kulambangra and Bougainville in the Solomon Islands it lives in the upper mountain forest at 2 000–3 000 meters. The Red Crossbill (*Loxia curvirostra*) feeds on larch in the Himalayas, on spruce in the Alps, and on pine in other restricted areas. The European cormorant (*Phalacrocorax carbo*) nests in inland areas of Europe and Asia (subspecies *sinensis*) on trees, while the Atlantic race (*carbo*) nests on the coast on rocks. The nominate subspecies of the Wilson's Warbler (*Wilsonia pusilla*) is found in Canadian bogs, while another race (*chryseola*) is found in warmer and drier habitats in the chaparral country of the west. These examples of striking changes in ecological characteristics could be matched by hundreds of additional ones, affecting food, habitat, nest site, altitudinal range, and others. Each of these changes involves populations within a single species.

The geographical variability of ecological preferences has been pointed out by many authors. In the Canada Jay (*Perisoreus canadensis*) two subspecies (*griseus* and *bicolor*) come into very abrupt contact apparently on account of ecological differences (Aldrich, 1943). Similar cases were described by Dementieff (1938) for Palearctic birds, although he apparently was in part deceived by allopatry of good species (see below). *Zonotrichia capensis* with its twenty-two subspecies lives under a remarkable range of environmental conditions, which varies from the hot and arid islands Curaçao and Aruba, the steamy lowlands of French Guiana and lower Amazonia to the mountains of Haiti, Costa Rica, and the Andes south to Tierra del Fuego. Many striking instances of geographical variation of ecological characters in the species *Dicrurus adsimilis, caerulescens, paradiseus, leucophaeus,* and *hottentottus* have been described by Vaurie (1949a). Many species of Palearctic birds that occur both in Britain and in the Canary Islands (Teneriffe) differ ecologically. This difference often consists in an apparently broader tolerance of the Teneriffe birds, which are able to occupy niches that are otherwise unoccupied in these islands with their much impoverished avifauna (Lack and Southern, 1949). The geographical variability of ecological requirements in the *Rhipidura rufifrons* group is remarkable (Mayr and Moynihan, 1946).

It is easy to see how such ecological diversification could permit populations of a species to re-enter the geographical range of other populations of the same species or species group without coming into actual contact. Johansen (1947) shows this for the *Phylloscopus trochilus* group which twice invaded the Caucasus. The western *abietinus,* which invaded the area from the north, is restricted to the forest of the lower slopes, the eastern *lorenzii* of the *neglectus* group, which invaded the Caucasus from the southeast is restricted to the subalpine forest zone. In the *Halcyon chloris* group there is an overlap on Palau between *chloris teraokai* which lives in the open country (near human habitations, etc.) and *cinnamomina pelewensis,* which is restricted to the true forest. In all these cases the original ecological differences had been acquired in geographical isolation, although no doubt they were further perfected during the period of contact.

These examples demonstrate the danger of reconstructing with too much confidence the past history of species on the assumption that a species is irrevocably tied to a single habitat. Animal species are not necessarily fixed components of biotic associations to the extent that the adherents of the biome concept want us to believe. This is abundantly proven by the striking variability of habitat preferences in many species of birds. And, if different subspecies in space can differ in their ecology, why not also subspecies in time?

In fact, there is good evidence that subspecies may change their ecology in time. There are numerous instances in birds where the range of a species was split by extrinsic factors into a western and eastern portion or into a northern and southern one. If there is a climatic difference in two sections, a gradual transformation of the isolated populations will occur with respect to their ecological tolerance and requirements. For instance, the species, which was the common ancestor of Nightingale (*Luscinia megarhynchos*) and Sprosser (*L. luscinia*) became separated into a southwestern (Mediterranean) and a northeastern (Russian–west Siberian) population. The southwestern birds became adapted to a dry, open, and hot kind of habitat, the northeastern birds to a more moist, more heavily forested and cooler habitat (Stresemann, 1948). The alteration occurred as a gradual change of the entire population. When subsequently the two populations expanded their ranges and came again into physical contact, they had not only acquired reproductive isolation but also ecological compatibility. In the zone of overlap *L. megarhynchos* occurs in open, dry locations, like gardens, parks, and cemeteries, while *L. luscinia* is restricted to lake shores, river bottoms, and swampy woods (Stresemann, l.c.).

Numerous similar examples have been recorded in the literature. The *Geokichla* of the Lesser Sunda Islands became separated into a western and an eastern group. The western group on the humid islands of Lombok, Sumbawa, and Flores became the humidity-loving forest species *G. dohertyi,* while the eastern group became the aridity-tolerant species *peronii* with headquarters on Timor. When rather recently *dohertyi* spread to Timor, it settled in the humid mountain forests where it is out of competition with *peronii,* inhabitant of the open monsoon forests of the lowlands.

Finally, one more case. During a late Pleistocene or post-Pleistocene arid period most of the bird life of Australia (except some desert species) was confined to a number of drought refuges along the coast (Gentilli, 1949; Mayr, 1950). In the tree runner *Neositta chrysoptera*, the two populations that were isolated in the west (southwestern Australia and Port Darwin region) were exposed to more severe aridity than the populations along the east coast of Australia. As a result, these two populations became much more drought tolerant than the eastern populations, and when conditions became again more humid the populations from these two western refuges were able to spread over most of Australia, while the eastern populations expanded their ranges only slightly. Here again, some of the populations changed materially during their isolation from others.

## Competition and Speciation

While Stresemann's studies had as their point of departure the minor or major ecological differences that are found among local populations, Lack in his studies started out from the ecological differences between species. He showed that these are not merely a negligible byproduct of speciation but rather that they are an indispensable prerequisite. Two species normally cannot co-exist in the same area unless they have sufficiently diverged in their ecological requirements so as not to be severe competitors (Lack, 1944, 1947a, 1949, etc.).

A consequence of this consideration is that ecological competition may prevent two perfectly good species from invading each other's ranges. The resulting geographical relationship of strict allopatry has often been interpreted as proving conspecificity. Stresemann (1939) cites many instances where complete or virtual allopatry does not prove conspecificity. In certain cases the presence of one species actually seems to keep out (or even drive out) another species from the area. For instance, *Ducula rosacea* seems to prevent *D. bicolor* from colonizing the small islets in the Lesser Sunda Islands, and *Tanygnathus megalorhynchus* seems to have crowded *T. sumatranus* off the small islands between Celebes and Sangir. In the African parrot genus *Agapornis* all the species are completely or almost completely allopatric (Moreau, 1948b). The realization that allopatry does not necessarily prove conspecificity has forced the taxonomist to re-examine all the more heterogeneous-appearing polytypic species. The result is that it was found, indeed, that some of them were composed of pseudo-conspecific allopatric species. Of the many cases of this sort I shall list here only a few that have recently come to my attention (Appendix). These cases are characterized by contiguity of populations without signs of intergradation, and often even a slight geographical overlap in the zone of contact.

### *Taxonomic consequences*

From the point of view of evolution the most important aspect of the ecological differences between local populations, subspecies, and species is that they set up selection pressures that lead to evolutionary divergence. This, in turn, results in an evolutionary divergence of taxonomic characters as discussed in the previous section.

Here we shall discuss the taxonomic effects of only one factor, namely competition. Lack (1947a) showed how competition determined which ecological niche the species *Geospiza magnirostris, difficilis, fuliginosa,* and *conirostris* occupy on a given island and how this, in turn, affects the size of the bill. The same phenomenon was shown by Amadon (1947) for two species pairs on Kauai Island. Of two species of the thrush *Phaeornis* that were thrown into competition one became a berry eater, the other an insect eater, and corresponding changes occurred in bill shape. Likewise, in the genus *Loxops* where the species *virens* comes into competition with the small-billed *parva* it has developed a subspecies with a noticeably heavier bill and different feeding habits. The two rock nuthatches (*Sitta tephronota* and *neumayer*) are very much alike in size outside their area of overlap, but one is much larger and the other much smaller in Iran where the two species are sympatric (Vaurie, 1950b).

In this manner ecological competition is one of the most potent factors in the modification of old and in the evolution of new taxonomic characters.

It is now evident that the study of the role of ecological factors has become one of the most important objects of taxonomy. Bird systematics is no longer merely the study of specimens in the museum, but rather, as the new systematics, it has shifted its main attention to the biological aspects of the taxonomic categories and it has expanded to include the study of animal populations in nature, of their evolution and relationships.

## The Significance of Ecological Factors for the Taxonomist

It is now realized that ecological characters are among the most important systematic characters of animals, in fact, that even morphological characters are usually merely indicators of genetic differences correlated with specific ecological conditions. The findings on ecological factors can then be summarized as follows:

(1) Every local population is slightly different from every other one in its ecological tolerance and requirements, just as every locality is slightly different from every other one.

(2) Within each population there is individual variability in many characters including ecological tolerance.

(3) Ecological characters appear to have largely a genetic basis, but there is also a considerable amount of non-genetic variability which is subject to conditioning.

(4) Species are rarely uniform ecologically. Subspecies often differ strikingly in ecological characteristics. Sometimes even morphologically monotypic species reveal a certain amount of geographical variablilty of ecological characters.

(5) Species must differ in their ecological requirements in order to be able to co-exist. The amount of difference that existed at the time of first overlap is augmented through natural selection.

(6) Competition affects the expression of morphological characters causing divergence in the zone of overlap of closely related species.

## Conclusion

Work on the geographical races of birds has led to the establishment of polytypic species and has helped to solve the riddle of the process of speciation. Emphasis is now shifting to the ecological factors that are active during this process of speciation and to the effect they have on taxonomic characters. These seem to be the most promising fields of future research in bird taxonomy, together with a study of the historical factors that have produced present distribution.

*Discussion:*

J. S. Huxley: I would like first of all to express my admiration for Dr Mayr's important and interesting paper, and my regret that he was unable to attend this Congress in person.

I would like to make a few comments.

(1) He stated that polymorphism always had a genetic basis, in the greater viability of a heterozygote, as suggested by Mr Fischer. This, however, is not the case. In the guillemot (*Uria aalge* var. *ringvia*) Prof. Fischer himself in a recent discussion expressed the opinion that the two forms

concerned were kept in balance by climatic factors, *ringvia* having an advantage in colder and moister climates. In other cases there may be an ecological balance of a different sort as with polymorphism in mimetic butterflies or in the balance between the greater hardiness of dominant melanics in moths, and the greater cryptic advantage of the normal form in non-industrial surroundings. Lloyd Morgan christened it "organic selection". This is not a very abbreviate phrase, but some brief term is required for the phenomenon, and I hope that evolutionists will find one.

(2) Dr Mayr referred to the importance of modifications of habit as often paving the way for genetic evolutionary change. I would hope that full credit will be given to Mr Baldwin and, C. Lloyd Morgan, who first drew attention to this phenomenon.[1]

(3) Dr Mayr stressed the adaptive nature of almost all characters, and the ever-present moulding force of natural selection. I would like to remind ornithologists of a beautiful set of instances, best illustrated in birds, where we can make an estimate of the selective forces at work, and then compare the results.

In truly polygamous birds, characters promoting successful mating by males ensure a multiple reproductive advantage: the sucessful male may have offspring by several females, while less successful males mate with only one or two or even none. Characters promoting success in holding territory in monogamous territorial species confer a unitary reproductive advantage, all successful males securing one mate, all unsuccessful no mate. Finally, purely epigamic (display) characters in such species confer a fractional reproductive advantage, the better equipped males having on the average a larger progeny. These differences in the strength of selection are clearly reflected in the degree of development of the characters concerned, exaggerated or so-called dystelic display characters only being seen with multiple advantage, while with fractional advantage they are never more than slightly developed. The distinctive characters advertising territory and conferring unitary advantage, whether they be visual or auditory, are always conspicuous but never exaggerated.

---

[1] The literature cited in this report covers the period since the 1938 Congress. — E. M.

## Appendix

### Pseudo-conspecific pairs of allopatric species

| | |
|---|---|
| 1. *Psittacula cyanocephala*<br>" *rosea* | Biswas, 1951, Amer. Mus. Novitates, no. 1500: 1–12. |
| 2. *Anthracoceros malabaricus*<br>" *coronatus* | Delacour, 1946, Zoologica, 31: 2. |
| 3. *Merops superciliosus*<br>" *philippinus* | Marien, 1950, Jour. Bombay Nat. Hist. Soc., 49 (2): 151–164. |
| 4. *Dendrocopos hardwickii*<br>" *canicapillus* | Greenway, 1943, Auk, 60: 564. |
| 5. *Ammomanes cinctura*<br>" *phoenicura* | Vaurie, 1951, Bull. Amer. Mus. Nat. Hist., 97: 431–526. |
| 6. *Melanocorypha calandra*<br>" *bimaculata* | Vaurie, 1951, Bull. Amer. Mus. Nat. Hist., 97: 431–526. |
| 7. *Pycnonotus aurigaster*<br>" *cafer* | Deignan, 1949, Jour. Washington Acad. Sci., 39: 273. |
| 8. *Coracina melaschista*<br>" *polioptera* | Deignan, MS. |
| 9. *Pericrocotus cantonensis*<br>" *roseus* | Deignan, MS. |
| 10. *Oenanthe hispanica*<br>" *pleschanka* | Vaurie, 1949, Amer. Mus. Novitates, no. 1425: 14–24. |
| 11. *Acrocephalus arundinaceus*<br>" *stentoreus* | Stresemann, E., and J. Arnold, 1949, Jour. Bombay Nat. Hist. Soc., 48: 428–443. |
| 12. *Turdoides caudatus*<br>" *altirostris* | Vaurie, MS. |
| 13. *Heterophasia capistrata*<br>" *melanoleuca* | Smythies, 1949, Ibis, 91: 637. |
| 14. *Lanius schach*<br>" *tephronotus* | Biswas, 1950, Jour. Bombay Nat. Hist. Soc., 49: 444–455. |
| 15. *Rhodopechys mongolica*<br>" *githaginea* | Vaurie, 1949, Amer. Mus. Novitates, no. 1424: 30–35. |
| 16. *Lonchura leucogaster*<br>" *leucogastroides* | Delacour, 1943, Zoologica, 28: 82. |
| 17. *Acridotheres cristatellus*<br>" *fuscus* | Marien, 1951, Jour. Bombay Nat. Hist. Soc., 49: 482–485. |
| 18. *Oriolus chinensis*<br>" *tenuirostris* | Delacour, 1951, L'OOiseau (in press). |

## References

Aldrich, J. W., 1943. Relationships of the Canada Jays in the northwest. Wilson Bull., 55: 217–222.

—— 1946 a. Significance of racial variation in birds to wildlife management. Jour. Wildlife Management, 10: 86–93.

—— 1946 b. Speciation in the white-cheeked geese. Wilson Bull., 58: 94–103.

Amadon, D., 1942. Notes on non-passerine genera. 2. Amer. Mus. Novitates, no. 1176: 1–12.

—— 1943. Notes on non-passerine genera. 3. Amer. Mus. Novitates, no. 1237: 1–22.

—— 1947. Ecology and the evolution of some Hawaiian birds. Evolution, 1: 63–68.

—— 1949. The seventy-five per cent rule for subspecies. Condor, 51: 250–258.

—— 1950. The Hawaiian honeycreepers (Aves, Drepaniidæ). Bull. Amer. Mus. Nat. Hist. 95: 157–262.

Bailey, A. M., 1948. Birds of Arctic Alaska. Colorado Mus. Popular Ser., no. 8: 151–155.

Bauer, H. and N. W. Timoféeff-Ressovsky, 1943. Genetik und Evolutionsforschung bei Tieren. In: Heberer, G., Die Evolution der Organismen, 335–429.

Behle, W. H., 1942. Distribution and variation of the Horned Larks (*Otocoris alpestris*) of western North America. Univ. California Publ. Zool., 46: 201–316.

Benson, C. W., 1946. On the change of coloration in *Lybius zombae* (Shelley). Bull. Brit. Ornith. Club, 67: 33–35.

—— 1948. Geographical voice-variation in African birds. Ibis, 90: 48–71.

Blanchard, B. D., 1941. The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. Univ. California Publ. Zool., 46: 1–178.

Bond, R. M., 1943. Variation in western sparrow hawks. Condor, 45: 168–185.

Brooks, M., 1942. Birds at the extremities of their ranges. Wilson Bull., 54: 12–16.

Bullough, W. S., 1942. On the external morphology of the British and continental races of starling (*Sturnus vulgaris* Linnaeus). Ibis, 84: 225–239.

Cain, A. J., 1952. Variation, selection, and speciation in the genus *Trichoglossus* (Aves, Psittaciformes).

Chapin, J. P., 1947. Color variation in shrikes of the genus *Chlorophoneus*. Auk, 64: 53–64.

—— 1948. Variation and hybridization among the Paradise Flycatchers of Africa. Evolution, 2: 111–126.

—— 1949. Relationship and voice in the genus *Calamocichla*. Ornith. Biol. Wiss., 7–16.

Chapman, F. M., 1940. The post-glacial history of *Zonotrichia capensis*. Bull. American Mus. Nat. Hist., 77: 381–438.

Cott, H. B., 1947. The edibility of birds. Proc. Zool. Soc. London, 116: 371–524.

Cushing, J. E., Jr., 1941. Non-genetic mating preference as a factor in evolution. Condor, 43: 233–236.

—— 1944. The relation of non-heritable food habits to evolution. Condor, 46: 265–271.

Delacour, J. and E. Mayr, 1945. The family Anatidae. Wilson Bull., 57: 1–55.

Dobzhansky, Th., 1941. Genetics and the origin of species. Columbia Univ. Press, New York, 446 pp.

Dunajewski, A., 1939. Gliederung und Verbreitung des Formenkreises *Lanius schach* L. Jour. Ornith., 87: 28–53.

Fisher, H. I., 1947. The skeleton of recent and fossil Gymnogyps. Pacific Science, 1: 227–236.

Gause, G. F., 1947. Problems of evolution. Trans. Conn. Acad. Arts, Sci., 37: 17–68.

Gentilli, J., 1949. Foundations of Australian bird geography. Emu, 49: 85–129.

Haartman, L. v., 1949. Der Trauerfliegenschnäpper I. Ortstreue und Rassenbildung. Act. Zool. Fenn., 56: 1–104.

Hawbecker, A. C., 1948. Analysis of variation in western races of the white-breasted nuthatch. Condor, 50: 26–39.

Hindwood, K. A. and E. Mayr, 1946. A revision of the stripe-crowned pardalotes. Emu, 46: 49–67.

Hoesch, W. and G. Niethammer, 1940. Die Vogelwelt Deutsch-Südwestafrikas. Jour. Ornith., Sonderh. 75–84.

Howard, H., 1947 a. An ancestral Golden Eagle raises a question in taxonomy. Auk, 64: 287–291.

—— 1947 b. A preliminary survey of trends in avian evolution from Pleistocene to recent time. Condor, 49: 10–13.

Huxley, J., 1942. Evolution. The modern synthesis. George Allen and Unwin Ltd., London, 645 pp.

Irwin, M. R., 1949. On immunogenetic relationships between the antigenic characters specific to two species of Columbidae. Genetics, 34: 586–606.

Jany, E., 1948. L'Influence de l'humidité du climat sur la coloration du plumage chez les pies-grieches grises de l'Afrique du Nord (*Lanius excubitor* L.). L'Oiseau, 18: 117–132.

Jepsen, G. L., G. G. Simpson, and E. Mayr, 1949. Genetics, paleontology, and evolution. Princeton University Press, 474 pp.

Johansen, H., 1945. Races of bean-geese. Dansk Ornith. Foren. Tidsskr., 39: 106–127.

—— 1946. Notes on systematics and distribution of the Yellow Wagtails (*Motacilla flava* L.). Dansk Ornith. Foren. Tidsskr., 40: 121–142.

—— 1947. Notes on the geographical variation of the chiffchaff (*Phylloscopus collybita* [Vieill.]). Dansk Ornith. Foren. Tidsskr., 41: 212–215.

Kullenberg, B., 1947. Über Verbreitung und Wanderungen von 4 *Sterna* Arten. Ark. Zool., 38 A, 17: 1–80.

Lack, D., 1944 a. Ecological aspects of species formation. Ibis, 86: 260–286.

—— 1944 b. Correlation between beak and food in the crossbill. Ibis, 86: 552–553.

—— 1945. The Galapagos Finches (Geospizinae). A study in variation. Occ. Pap. California Acad. Sci., 21: 1–158.

—— 1946. The taxonomy of the robin *Erithacus rubecula* (Linn.). Bull. Brit. Ornith. Club, 66: 55–65.

—— 1947 a. Darwin's finches. Cambridge Univ. Press, 208 pp.

—— 1947 b. A further note on the taxonomy of the robin *Erithacus rubecula* (Linnaeus). Bull. Brit. Orn. Club, 67: 51–54.

—— 1947 c. The significance of clutch size. Ibis, 89: 302–352.

—— 1949. The significance of ecological isolation. In: Genetics, paleontology, and evolution by G. L. Jepsen, G. G. Simpson, and E. Mayr, 1949, Princeton University Press, 299–308.

Lack, D. and H. N. Southern, 1949. Birds on Tenerife. Ibis, 91: 607–626.

Leopold, A. S., 1944. The nature of heritable wildness in turkeys. Condor, 46: 133–197.

Løppenthin, B., 1943. Systematic and biologic notes on the Long-tailed Skua, *Stercorarius longicaudus* Vieill. Medd. Grønland, 131 (12): 1–26.

Manning, T. H., 1942. Blue and Lesser Snow Geese on Southampton and Baffin Islands. Auk, 59: 158–175.

Marshall, J. T., Jr., 1948. Ecological races of song sparrows in the San Francisco Region. Condor, 50: 193–215, 233–256.

Mayaud, N., 1940. Considérations sur les affinités et la systématique de *Larus fuscus* et *Larus argentatus*. Alauda, 12: 89–98.

MAYR, E., 1941. Die geographische Variation der Färbungstypen von *Microscelis leucocephalus*. Jour. f. Ornith., 89: 377–392.

—— 1942 a. Systematics and the origin of species. Columbia University Press, New York, 334 pp.

—— 1942 b. Speciation in the junco. Review of speciation in the avian genus Junco by Alden H. Miller. Ecology, 23 (3): 378–379.

—— 1943. Criteria of subspecies, species, and genera in ornithology. Ann. New York Acad. Sci., 44: 133–140.

—— 1944. The birds of Timor and Sumba. Bull. Amer. Mus. Nat. Hist., 83: 123–194.

—— 1946. The number of species of birds. Auk, 63: 64–69.

—— 1947. Ecological factors in speciation. Evolution, 1 (4): 263–288.

—— 1948 a. The bearing of the new systematics on genetical problems. The nature of species. Advances in Genetics, 2: 205–237.

—— 1948 b. Geographic variation in the Reed-Warbler. Emu, 47: 205–210.

—— 1948 c. Climatic races in plants and animals. Evolution, 2 (4): 375–376.

—— 1949 a. Speciation and systematics. Genetics, Paleontology, and Evolution, Princeton University Press, 281–298.

—— 1949 b. Geographical variation in *Accipiter trivirgatus*. Amer. Mus. Novitates, no. 1415: 1–12.

—— 1949 c. Artbildung und Variation in der *Halcyon-chloris*-Gruppe. Ornith. Biol. Wiss., 54–60.

—— 1949 d. Speciation and selection. Proc. Amer. Phil. Soc., 93 (6): 514–519.

—— 1950. Notes on the genus *Neositta*. Emu, 49 (4): 282–291.

—— 1951. Report of the chairman of the Standing Committee on Terrestrial Faunas of the Inner Pacific. Proc. Pacific Sci. Cong. (in press).

MAYR, E., and D. AMADON, 1947. A review of the Dicaeidae. Amer. Mus. Novitates, no. 1360: 1–32.

MAYR, E., and M. MOYNIHAN, 1946. Evolution in the *Rhipidura rufifrons* group. Amer. Mus. Novitates, no. 1321: 1–21.

MAYR, E., and C. VAURIE, 1948. Evolution in the family Dicruridae. Evolution, 2: 238–265.

MAYR, E., and E. STRESEMANN, 1950. Polymorphism in the chat genus *Oenanthe* (Aves). Evolution 4 (4): 291–300.

MEINERTZHAGEN, R., 1950. Some problems connected with Arabian birds. Ibis, 92: 336–340.

MILLER, A. H., 1940. Climatic conditions of the Pleistocene reflected by the ecologic requirements of fossil birds. Proc. Sixth Pac. Sci. Congress Berkeley, 2: 807–810.

—— 1941. Speciation in the avian genus Junco. Univ. California Publ. Zool., 44: 173–434.

—— 1947. Panmixia and population size with reference to birds. Evolution, 1: 186–190.

—— 1949. Some ecologic and morphologic considerations in the evolution of higher taxonomic categories. Ornith. Biol. Wiss., 84–88.

MOREAU, R. E., 1948 a. Some recent terms and tendencies in bird taxonomy. Ibis, 90: 102–111.

—— 1948 b. Aspects of evolution in the parrot genus *Agapornis*. Ibis, 90: 206–239.

PALMGREN, P., 1942. Die Populationsgrösse der Vögel als Evolutionsfaktor. Naturwissenschaften, 30: 217–220.

PALUDAN, K., 1940. Contributions to the ornithology of Iran. Danish Sci. Investig. Iran, pt. 2: 11–54.

PATEFF, P., 1947. On the systematic position of the starlings inhabiting Bulgaria and the neighbouring countries. Ibis, 89: 494–507.

Peitzmeier, J., 1942. Die Bedeutung der oekologischen Beharrungstendenz für faunistische Untersuchungen. Jour. f. Ornith., 90: 311–322.

Petersen, N., and K. Williamson, 1949. Polymorphism and breeding of Rock Dove in the Faeroe Islands. Ibis, 91: 17–23.

Pitelka, F. A., 1945 a. Differentiation of the Scrub Jay, *Aphelocoma coerulescens*, in the Great Basin and Arizona. Condor, 47: 23–26.

—— 1945 b. Pterylography, molt, and age determination of American jays of the genus *Aphelocoma*. Condor, 47: 229–260.

Rand, A. L., 1943. *Larus kumlieni* and its allies. Canadian Field Nat., 56: 123–126.

—— 1948. Glaciation, an isolating factor in speciation. Evolution, 2: 314–321.

Rand, A. L., and M. A. Traylor, 1950. The amount of overlap allowable for subspecies. Auk, 67: 169–183.

Rensch, B., 1943. Die biologischen Beweismittel der Abstammungslehre. In: Heberer, G., Die Evolution der Organismen, 57–85.

—— 1947. Neuere Probleme der Abstammungslehre. Die Transspezifische Evolution, Stuttgart, 407 pp.

Ripley, S. D., 1941. Notes on the genus *Coracina*. Auk, 58: 381–395.

—— 1944. The bird fauna of West Sumatra islands. Bull. Mus. Comp. Zoöl., 94: 305–430.

—— 1945. Suggested terms for the interpretation of speciation phenomena. Jour. Washington Acad. Sci., 35: 337–341.

—— 1949. Avian relicts and double invasions in peninsular India and Ceylon. Evolution, 3: 150–159.

Ripley, S. D., and H. Birckhead, 1942. Birds collected during the Whitney South Sea Expedition 51. On the fruit pigeons of the *Ptilinopus purpuratus* group. Amer. Mus. Novitates, no. 1192: 1–14.

Salomonsen, F., 1944. The Atlantic Alcidae. Göteborgs Vetensk. Samh. Handl. (6) 3 B 5: 1–138.

Serventy, D. L., 1943. The white phase of the Giant Petrel in Australia. Emu, 42: 167–169.

Simpson, G. G., 1944. Tempo and mode in evolution. Columbia Univ. Press, New York, 237 pp.

Snyder, L. L., and T. M. Shortt, 1946. Variation in *Bonasa umbellus*, with particular reference to the species in Canada east of the Rockies. Canadian Jour. Res., D 24: 118–133.

Southern, H. N., 1943. The two phases of *Stercorarius parasiticus* (Linnaeus). Ibis, 85: 443–485.

—— 1944. Dimorphism in *Stercorarius pomarinus* (Temminck). Ibis, 86: 1–16.

—— 1946. The inheritance of head colour in the Gouldian Finch (*Poephila gouldiae* Gould). Avicult. Mag. London, 52: 126–131.

Southern, H. N., and E. C. R. Reeve, 1942. Quantitative studies on the geographical variation of birds — The Common Guillemot (*Uria aalge* Pont.). Proc. Zool. Soc. London 111 A: 255–276.

Southern, H. N., and D. L. Serventy, 1947. The two phases of *Astur novae-hollandiae* (Gm.) in Australia. Emu, 46: 331–347.

Steinbacher, G., 1948. Der Einfluss der Eiszeit auf die europäische Vogelwelt. Biologisches Zentralblatt, 67: 444–456.

Steinbacher, G., and J. Steinbacher, 1943. Über die Entstehung und das Alter von Vogelrassen. Zool. Anz., 141: 141.

Stresemann, E., 1939. Die Vögel von Celebes. Teil I. Jour. f. Ornith., 88: 1–135; 389–487.

—— 1940. Zur Kenntnis der Wespenbussarde. Arch. Naturg., NF. 9: 137–193.

—— 1943 a. Oekologische Sippen-, Rassen- und Artunterschiede bei Vögeln. Jour. f. Ornith., 91: 305–324.

—— 1943 b. *Cracticus rufescens* De Vis. Ornith. Monatsb., 51: 68–72.

STRESEMANN, E., 1948. Nachtigall und Sprosser: ihre Verbreitung und Ökologie. Ornith. Berichte, 1: 193–222.

STRESEMANN, E., and N. W. TIMOFÉEFF-RESSOVSKY, 1947. Artenstehung in geographischen Formenkreisen I. Der Formenkreis *Larus argentatus-cachinnans-fuscus*. Biol. Zentralbl., 66: 57–76.

STRESEMANN, E., and J. ARNOLD, 1949. Speciation in the group of Great Reed-Warblers. Jour. Bombay Nat. Hist. Soc., 48 (3): 428–443.

SUTTER, E., 1946. Die Flügellänge junger und mehrjähriger Grünfinken und Gartenrötel. Ornith. Beob., 43: 72–85.

SUTTON, G. M., 1938. Oddly plumaged orioles from western Oklahoma. Auk, 55: 1–6.

THOMSON, A. L. et al., 1943. Physiological races in birds. Bull. Brit. Ornith. Club, 63: 73–80.

THORPE, W. H., 1945. The evolutionary significance of habitat selection. Jour. Animal Ecol., 14: 67–70.

TIMOFÉEFF-RESSOVSKY, N. W., 1943. [Discussion of Stresemann 1943 a.] Jour. f. Ornith., 91: 326-327.

TODD, W. E. D., and H. FRIEDMANN, 1947. A study of the gyrfalcons with particular reference to North America. Wilson Bull., 59: 139–150.

VAURIE, C., 1949 a. A revision of the bird family Dicruridae. Bull. Amer. Mus. Nat. Hist., 92: 205–342.

—— 1949 b. Notes on the bird genus *Oenanthe* in Persia, Afghanistan, and India. Amer. Mus. Novitates, no. 1425: 1–47.

—— 1950 a. Notes on some Asiatic titmice. Amer. Mus. Novitates, no. 1459: 1–66.

—— 1950 b. Notes on Asiatic nuthatches and creepers. Amer. Mus. Novitates, no. 1472: 1–39.

VOOUS, K. H., 1947. The history of the distribution of the genus *Dendrocopos*. Amsterdam, 142 pp.

—— 1949. Distributional history of Eurasian bullfinches, genus *Pyrrhula*. Condor, 51: 52–81.

VOOUS, K. H., and J. G. VAN MARLE, 1949. The distributional history of *Coracina* in the Indo-Australian Archipelago. Bijdragen tot de Dierk., 28: 513–529.

WHITE, C. M. N., 1948. Size as a racial character. Bull. Brit. Ornith. Club, 69: 11–13.

ZEUNER, F. E., 1943. Studies in the systematics of Troides Hübner (Lepidoptera Papilionidae) and its allies, distribution, and phylogeny in relation to the geological history of the Australian Archipelago. Trans. Zool. Soc. London, 25: 107–184.

# Der Einfluss philosophischer Naturbetrachtung auf die ornithologische Systematik

*Erwin Stresemann*

*Zoologisches Museum, Berlin*

Seitdem durch Darwin die historische Betrachtungsweise eingeführt wurde, hat man sich daran gewöhnt, die Systematik als eine Erfahrungswissenschaft anzusehen. Wir verfolgen den Werdegang der Artbildung von seinem ersten Beginn an und suchen die Ursachen auf, welche die Differenzierung herbeiführen. Die Ergebnisse, die das Studium der niedersten Stufen, der Mutanten, der Populationen, der geographischen Rassen lieferte, können dann dazu dienen, die historischen Zusammenhänge zwischen den höheren Einheiten zu beurteilen, nämlich zwischen den Spezies, Gattungen, Ordnungen, die uns nur als Abstraktionen gelten.

Die Bemühungen des Menschengeistes, die Vielfalt der Erscheinungen zu ordnen und zu deuten, mussten am anderen Ende, also bei den höheren Kategorien, beginnen. Den Abschluss einer langen vorwissenschaftlichen Entwicklung und den grossartigen Beginn einer wahren Naturwissenschaft bedeuten die Schriften des Aristoteles. Im Bestreben, den schroffen Gegensatz zur Empirie zu überbrücken, in den die griechische Philosophie durch die Gedankensysteme der Eleaten und Platons geraten war, gelangte Aristoteles zu der Vorstellung, dass alles Belebte zweckmässig gestaltet sei, und zwar darum, weil die beiden Prinzipien Materie und Idee zusammenwirkend eine Einheit bilden, wobei die Idee, als der in der Materie wirkende Naturzweck, den Stoff nach sich entwickelt und gestaltet. Die Idee ist das Urbild, das Geschöpf ist dessen Abbild. Die Welt ist ein Stufenreich solcher Zweckbestimmungen, das von den niedrigsten Erscheinungen zu den höchsten emporführt. Da nun die Ideen ewig und unveränderlich sind, müssen es auch die von ihnen hervorgerufenen Gestaltungen sein.

Nach der Lehre des Aristoteles formt sich also die Gestalt nach dem Bedürfnis, folglich hat das Bedürfnis in der Stufenfolge der Dinge einen höheren Rang inne als die Form. Eines seiner Beispiele ist das folgende: Wenn eine Henne einen Hahn besiegt hat, dann beginnt sie zu krähen und ahmt die Hähne nach, indem sie andere Hennen zu treten sucht. Die so veränderten Triebe haben zur Folge, dass die Henne Hahnengefieder annimmt.

Aus dieser Auffassung des Aristoteles ergeben sich seine Ordnungsprinzipien. Dadurch, dass er die Vögel ökologisch kennzeichnet, glaubt er auch die wesentlichen Merkmale ihrer Gestalt zu erfassen. Er schlägt vor, sie in drei Gruppen zu gliedern: 1. Landvögel, 2. Wasservögel, 3. Vögel, die an Flüssen, Seen oder Meeren leben. Die ersten haben ja zwangsläufig Lauf-, Sitz- oder Kletterfüsse, die zweiten Schwimmfüsse, die dritten Spaltfüsse mit langen Zehen. Die Landvögel lassen sich ihrerseits in mehrere Funktionsgruppen einteilen, darunter Wurmfresser, Distelfresser, Fresser von Holzkäferlarven.

Die aristotelischen Richtlinien sind für die Renaissance-Zoologen massgebend geblieben. Belon 1555 hat sie befolgt, indem er die Vögel gliederte in solche, die vom Raub leben, in Schwimmvögel, spaltfüssige Sumpfvögel (wozu er auch Eisvögel und Bienenfresser stellte), in Bodenvögel (Strauss, Hühner, Lerchen usw.), ferner in grosse Wald- und Buschvögel und kleine Wald- und Buschvögel. Den letzteren fügt er auch die Schwalben an.

Aldrovandi 1599 bemüht sich, dieses System zu verbessern. Er führt neue diagnostische Merkmale ein, die er dem Verhalten entnimmt. Eine besondere Gruppe bilden in seinem System die gutsingenden Vögel, nämlich die Finken, Lerchen und der Kanarienvogel; eine zweite Gruppe die Vögel, die sich nur im Staub baden; eine weitere Gruppe diejenigen, die sich in Staub oder Wasser baden, nämlich die Tauben und die Ammern.

Bis tief ins 17. Jahrhundert hat sich die auf Aristoteles fussende Systematik erhalten können. Mit strenger Konsequenz ist sie zuletzt von Walter Charleton, Leibarzt Karls II., in seinem Onomasticon zooicon 1668 durchgeführt worden.

Nach Charleton gibt es 2 Hauptabteilungen: Landvögel und Wasservögel. Die Landvögel zerfallen in Fleischfresser, Insektenfresser, Körnerfresser, Beerenfresser. Die Wasservögel zerfallen in ruderfüssige und spaltfüssige, und die letzteren ihrerseits in Fischfresser, Insektenfresser und Krautfresser.

Die insektenfressenden Landvögel gliedert Charleton in zwei Gruppen: in singende und nicht singende, die körnerfressenden Landvögel in drei Gruppen, nämlich in solche, die im Staub baden, in solche, die in Staub und Wasser baden, und drittens in singende.

Wie sehen nun diese Haufen aus? Einige Beispiele werden es zeigen:

Unter den fleischfressenden Landvögeln finden sich zusammen Aquila, Collurio, Cuculus, Psittacus, Corvus, Bubo, Caprimulgus, Struthio und Vespertilio, die Fledermaus! Im Staub badende Körnerfresser sind Gallus, Otis, Oedicnemus, Ortygometra etc., im Staub und Wasser badende dagegen Columba, Passer und Troglodytes.

Was hätte wohl deutlicher beweisen können, dass die aristotelischen Grundsätze für ein System der Vögel nichts taugen, als dieser Anordnungsversuch, gegen den sich der gesunde Sinn sträuben musste?

Die Reaktion lässt nicht lange auf sich warten. 1676 erscheint, gleichfalls in London, Francis Willughby's posthumes Werk „Ornithologiae libri tres" und wirft die 2000 Jahre alte klassische Systematik endlich über den Haufen, um eine neue an ihre Stelle zu setzen, die sich nicht an die Funktion, sondern an die Form hält. Als wichtigste Kriterien dienen dem Revolutionär Schnabelgestalt, Fussbau und Körpergrösse. Nach vorwiegend morphologischen Merkmalen unterteilt er die Vögel so lange, bis geschlossene Endgruppen übrig geblieben sind, die vielfach sogar vor der heutigen Systematik noch bestehen können, z. B. die Fringillinae, die Corvinae, die Turdinae, die Psittaci, die Gallinae, die Limosugae (fast genau entsprechend unseren Limicolae), die Steganopodes usw.

Lange Zeit blieb dieses rein empirische System unübertroffen, mochten es auch eifrige Besserwisser bald wieder umstossen. Es bildet die wahre Verwandtschaft weit richtiger ab, als das sogenannte „natürliche System", das 60 Jahre später von Linnaeus ersonnen worden ist. Wir wollen hier die teilweise auf Willughby aufbauenden klassifikatorischen Versuche von Barrère 1745, Klein 1750 und Möhring 1752 übergehen und uns gleich dem Genius der Organisation zuwenden, dessen Schriften den Lauf der ornithologischen Taxonomie jahrzehntelang bestimmt haben: Carolus Linnaeus, der schon in der ersten Auflage seines Systema Naturae, 1735, eine neue Hierarchie der Begriffe einführte: Classis, Ordo, Genus, Species, Varietas.

Linnaeus fasst in der sog. 6. Auflage des Systema Naturae (Stockholm 1748) alle ihm bekannten Vogelarten in 85 Genera zusammen, die er, wie schon 1735, auf nur 6 Ordnungen verteilt. Was ihn dabei leitet, sind keineswegs die Gesichtspunkte eines Willughby. Dieser (bezw. sein Freund John Ray) hatte offensichtlich den Gesamteindruck des Vogels zum Gradmesser der Affinität gewählt und sich nicht gescheut, kleine Gruppen abzusondern, wenn es der Habitus so verlangte. Linnaeus dagegen legt Wert darauf, ein übersichtliches, ebenmässiges und daher einprägsames System aufzustellen. Wenn man, wie er, die Kennzeichen hauptsächlich vom Schnabel und in zweiter Linie von den Füssen nahm, konnte man beliebig viele grosse Haufen, sogenannte Ordnungen, bilden. Linnaeus entschied sich für die Zahl 6. Solch ausgeklügelte Beschränkung zwang ihn zu wunderlichen Kombinationen.

Es war ein Glück für die Entwicklung der Ornithologie, dass sie damals nicht der alleinigen Einwirkung des linnaeischen Geistes ausgesetzt blieb, sondern zu gleicher Zeit auch aus anderer, ja geradezu entgegengesetzter Richtung gefördert wurde. Linnés grosser Antipode Buffon, im gleichen Jahr wie er geboren, nämlich 1707, war der Überzeugung, dass die „nomenclateurs“ der Naturkunde schweren Schaden zufügten, indem sie die Ordnung der Dinge in falschem Lichte zeigten und durch ihre trockne Methodik die Aufmerksamkeit von den eigentlichen Aufgaben des Forschers auf Unwesentliches, ja auf die Produkte ihrer eigenen Willkür ablenkten. Für Buffon sind die Species keineswegs durch Gottes Hand nach einem Schöpfungsplan geformt und daher scharf abgegrenzt und unveränderlich. Vielmehr vermutet er die Existenz einer Anzahl von fundamentalen Typen und ihre allmähliche Vervielfältigung durch Bastardierung, durch Degeneration und durch lokale Einflüsse der Nahrung und des Klimas. Je kleiner eine Vogelart sei, umso grösser sei die Zahl ihrer nahen Verwandten; man könne annehmen, dass sie alle von einer gemeinsamen Wurzel abstammen. Unter den kleinen Vögeln scheinen ihm viele sogenannte Species nichts anderes als klimatische Varietäten zu sein. Der europäische Grauwürger z. B. bilde in Europa zwei Varietäten, eine grosse (den Raubwürger) im Norden und eine kleine (den Schwarzstirnwürger) in Frankreich, was wahrscheinlich mit Unterschieden in der Nahrungsmenge zusammenhänge. Es sei daher keineswegs zu verwundern, dass der europäische Grauwürger unter entfernteren Himmelsstrichen noch stärker abändere.

Wer wie Buffon glaubte, im Tierreich an vielen Stellen Übergänge zu bemerken, nicht nur zwischen den höheren Gruppen, sondern auch zwischen den Arten, musste Linnés hierarchische Nomenclatur verurteilen. In leichter Übertreibung einer richtigen Idee behauptet Buffon: Je weiter man bei der Aufteilung der Naturprodukte geht, umso mehr wird man sich der Wahrheit nähern, denn in Wirklichkeit gibt es in der Natur nur Individuen; die Genera, die Ordnungen und die Klassen existieren nur in unserer Einbildung.

Viele Ornithologen haben damals gemeint, es bleibe ihnen nichts weiter übrig, als sich für eine der beiden Richtungen zu entscheiden, da sie die Gegensätze für unvereinbar hielten. Der erste Zoologe, dem ihre Synthese glückte, war Pallas. Von dessen Schriften beeinflusst ist 1788 einer aufgetreten, dessen Weitblick die endliche Verschmelzung zu einer wahren Naturgeschichte voraussah, und der sie dem Fortschritt zuliebe dringend forderte. Das war ein Schüler Blumenbachs, der Göttinger Zoologe Blasius Merrem, der in der Vorrede zu seinem „Versuch eines Grundrisses zur allgemeinen Geschichte und natürlichen Eintheilung der Vögel“ auseinandersetzte: „Die

Naturgeschichte soll, wie schon ihr Name lehrt, eine historische Kenntniss seyn. Beobachtungen und Erfahrungen, nicht Vernunftschlüsse müssen also der Grund sein, worauf sie sich stützt. Alles was von dem Aufenthalte, dem Wachstum, der Vermehrung, den Eigenschaften der Thiere und überdies alles, was von ihrer Lebensart, ihren Sitten und Trieben bekannt ist, muss aufs Sorgfältigste bemerkt, die Körper selbst aufs Genaueste in verschiedenen Lagen beobachtet und ihr Verhalten in denselben untersucht werden. Nur so können wir Stoff zu den ersten Grundlinien einer allgemeinen Naturwissenschaft ziehen, in der die wesentlicheren Eigenschaften durch Vergleichung vieler Körper unter einander von den unwesentlicheren abgesondert und dadurch gewiesen werden kann, worin die mannigfaltigen Arten der Geschöpfe näher mit einander übereinstimmen oder weiter von einander abweichen".

Merrems Gedankengänge wurden von dem grossen Reformator des Vogelsystems, Carl Illiger, befolgt, der schon im Jahre 1800 den Begriff des Genus folgendermassen definierte: ,,Gattung ist die Zusammenstellung der im Habitus übereinstimmenden Arten. Den künstlichen, nur nach einzelnen Merkmalen unterschiedenen Gattungen widerstrebt unser Gefühl". Und beeinflusst durch die philosophischen Bedenken, die Kant 1790 gegen Buffons Transmutationslehre vorgebracht hatte, fährt Illiger fort: ,,So sehr man auch geneigt sein möchte, zu glauben, die Arten einer Gattung wären aus einem gemeinschaftlichen Urstamme entsprossen und durch dieses Band der Verwandtschaft an einander geknüpft, so müssen wir dieses doch als einen unerweislichen, ja der Natur der Art widersprechenden Satz dahingestellt sein lassen, bis uns einst mehr Beobachtungen den Schlüssel zu dem Geheimnis der Natur geben werden, wie sie Arten erzeugt, und wie sie zufällig entstandene und durch äusserliche Einflüsse hervorgebrachte Abändrungen zu erblichen Abarten macht; und wir müssen uns an die Sache halten, so wie wir sie jetzt finden. Da wir in der Natur wirklich finden, dass mehrere Arten in ihrem Habitus sehr übereinkommen, und von andern sich unterscheiden, und da wir sehen, dass eine Art durch diese grössere Übereinstimmung mit einer Anzahl von Arten in näherer Verwandtschaft steht, als mit irgendeiner andern; so ist es ein ganz natürlicher Schluss, dass wir annehmen, die Natur selbst habe diese Haufen gebildet."

So hatte es also den Anschein, als werde die weitere Entwicklung in der Ornithologie zwangsläufig zum Studium der Varietäten und ihrer Verursachung führen, gemäss dem Satz des Pallas ,,Varietates nullas neglexi, quae in Zoologia maximi momenti certae sunt" — aber es kam zunächst anders! Um die gleiche Zeit, in der Illiger wirkte, hatte Schelling begonnen, seine Lehre von der metaphysischen Ordnung des Alls und den in der Natur repräsentierten Urbildern zu verbreiten. Seine Dogmen erzeugten unter den jungen Naturforschern einen wahren Massenwahn. Nicht nur in den Arten, sondern auch in den höheren Kategorien erblickten Schellings Schüler die Manifestierung von ewigen Urbildern, also Glieder eines harmonischen Weltgefüges, dessen Struktur es nun zu erforschen galt. Sie fassten die Gattungen, Ordnungen, Klassen als unveränderliche Realitäten auf, obwohl sie sich nicht, wie die Individuen, durch ihre greifbare Erscheinung, sondern nur in der Idee darbieten, denn für Schelling war, wie für Platon und seine geistigen Vorläufer, Denken und Sein identisch. Einer von Schellings eifrigsten Schülern, der Münchner Zoologe Spix, wendet sich 1811 mit pathetischen Worten gegen Illiger und Lamarck, die erklärt hatten, dass diese architektonische Verkettung der Geschöpfe nicht in der Natur begründet, sondern das Produkt einer blossen Willkür und Erdichtung der Naturforscher sei, dass es weder Reiche noch Klassen, weder Familien noch Gattungen in der Natur, sondern allein in den Köpfen der Gelehrten gäbe. „Welches Heil", ruft Spix aus, „welches Heil für die Naturgeschichte, wo man zuletzt statt Ordnung einen blossen Zufall, statt der unabänderlichen Gesetzmässigkeit in der Natur nur seine imaginäre Willkür anerkennt! Gleich wie der thierische Körper durch Organe, der menschliche Staat oder die militärische Gesellschaft durch Dignitäten gegliedert ist, ebenso sind es in der Natur die Thiere untereinander."

Wir können uns hier nicht damit aufhalten, die weitere Entwicklung der Naturphilosophie zu verfolgen, die namhafte Ornithologen in Deutschland und England Jahrzehnte lang mit ihrem falschen Schein geblendet hat. Auch wer sich von ihr nicht in die Bereiche uferloser Spekulation entführen lies, blieb dennoch ihrem Einfluss ausgesetzt. Die von Owen und manchen seiner Zeitgenossen in England und Deutschland vertretene Typenlehre ist eine verkappte Naturphilosophie. Selbst Strickland, ein erklärter Gegner aprioristischer Spekulation, meint 1840: die Species seien nicht absolut, sondern relativ geschaffen, nämlich nicht nur mit Bezug auf die ihnen zugedachte Lebensweise, sondern auch mit Bezug auf andere Spezies, denen die Schöpfung ähnliche, aber nicht identische Aufgaben zugedacht hat. Dadurch lasse sich die Existenz von Verwandtschaftsgruppen erklären. Diese verschiedenen Gruppen könne man als ebenso viele Realisationen einer abstrakten Idee betrachten, von welcher der Schöpfer selbst in den ungewöhnlichsten und excentrischsten Modifikationen der Form nicht abwich.

Es war also hier, im Einklang mit den Lehren der Naturphilosophie, von der Denkmöglichkeit der Artumwandlung keine Rede mehr; ja die Naturphilosophen hatten sogar bewirkt, dass die Varietäten wieder als konstante Bildungen angesehen wurden. Dieser Überzeugung war z. B. der eifrigste Varietätensammler jener Zeit, Christian Ludwig Brehm. 1853 äussert er die Meinung, dass die Subspecies nicht aus den ,,ächten" Arten durch Vermehrung und Verbreitung der Individuen hervorgegangen sind, er glaubt vielmehr, ,,dass, da wir in dem standhaften Festhalten der Bildung der Geschöpfe eine wunderbare und dauernde Regel deutlich wahrnehmen, diese Subspecies von Anbeginn aus Gottes unbegreiflicher Schöpferkraft hervorgegangen sind und auch so bleiben werden, wie sie sind". Der gleichen Ansicht huldigte bis an sein Lebensende Brehms geistiger Zögling Hermann Schlegel. Er sah noch 1878 in den geographischen Abänderungen keineswegs die heranwachsenden, etwa durch klimatische Einflüsse geförderten Keime neuer Species, sie galten ihm vielmehr als ,,Conspecies", d. h. als lokale und unveränderliche Ausprägungen des Typus der unveränderlichen Species. Denn nicht umsonst hatte Hartlaub 1852 den Ornithologen eingeschärft: ,,Möchte doch in der Systematik alles vermieden werden, wodurch der Stabilität des Begriffes Art irgendwelche Beeinträchtigung droht". Sieben Jahre später ist diese Bedrohung wieder aufgestiegen, furchtbarer denn je, denn Darwin hatte die These aufgestellt: ,,Der einzige Unterschied zwischen Arten und ausgebildeten Varietäten besteht darin, dass die letzten durch erkannte oder vermutete Zwischenstufen noch heutzutage mit einander verbunden sind und die ersten es früher gewesen sind. Wir werden die Arten auf dieselbe Weise zu behandeln haben wie die Naturforscher jetzt die Gattungen behandeln, welche annehmen, dass die Gattungen nichts weiter seien als willkürliche, der Bequemlichkeit halber eingeführte Gruppierungen. Das mag nun keine eben sehr heitere Aussicht sein, aber wir werden hierdurch endlich das vergebliche Suchen nach dem unbekannten und unentdeckbaren Wesen der Spezies loswerden."

Es hat dann, infolge des zähen Widerstandes der älteren Generation, noch Jahrzehnte gedauert, bis es den Ornithologen gelang, auf evolutionistischer Grundlage eine einigermassen brauchbare Speziesdefinition zu formulieren, und bis sie nun endlich aufhörten durch den gespenstischen Zweifel geängstigt zu werden, ob diese oder jene Form eine wirkliche Art oder eine Varietät sei.

Damit war der Naturphilosophie freilich noch immer nicht der Lebensnerv durchschnitten worden, wenigstens nicht in Deutschland, ihrer Wiege; und wir begegnen sogar im Programm dieses Kongresses dem Titel eines Vortrages, der uns über ,,The real limits of genus" unterrichten wird. Fast wider mein eigenes Erwarten kann also mein historischer Rückblick, obwohl er ums Jahr 1860 endet, Anspruch darauf erheben, von aktuellem Interesse zu sein.

# A Sixteenth Century Classification of Birds

*Elsa G. Allen*

*Cornell University, Ithaca N.Y.*

Several years ago I saw in Alfred Newton's Dictionary of Birds a reference to an ornithological treatise by the Dutch anatomist Volcher Coiter. Very few copies of this work exist and only three are in the United States. One of these is preserved in the Library of the Surgeon General in Washington.

On my next trip to Washington I went to this Library in order to see it, but as it was during the war, this was not permitted and, as a matter of fact, the tract had been moved to a place of greater safety.

Three years later it was possible to have it microfilmed. The whole work is entitled, "De Avium Sceletis et Praecipuis musculis", and the second chapter, my particular interest, bears the heading, "De Differentiis Avium". The entire work is but little known, because it is bound in the middle of a group of lecture notes[1] assembled by Volcher Coiter when he was attending Fallopius' Course in Anatomy at the University of Padua. The publication date is 1575.

The treatise is divided into twelve chapters, occupying fourteen pages written in the Latin of the Sixteenth Century. I am greatly indebted to a linguist friend, Miss Ethel Davis, for rendering the second chapter, the De Differentiis Avium, into English.

The substance of the other chapters is given to show the scope of Coiter's knowledge of bird structure and anatomy — his laboratory knowledge we may call it.

Chapter 1. discusses the skeletons of birds in general with some remarks on Aristotle's interpretations of the structure of birds.

Chapter 3. concerns the Bird's Cranium.
Chapter 4. » » » Neck.
Chapter 5. » » » Breast.

---

[1] The Lectiones Gabrielis Fallopii.

Chapter 6. concerns the Bird's Clavicle.
Chapter 7. » » » Scapula.
Chapter 8. » » » Sternum.
Chapter 9. » » » Upper or fore ribs.
Chapter 10 » » » Lumbar bones, the sacrum, ilium, hip and pubis.
Chapter 11 » » » bones of the wing and method of flying.
Chapter 12 » » » bones of the shin or shank, and foot bones.

The text on all of these headings indicates that Coiter knew and understood the way a bird's skeleton functions, and the drawings of several types of skeletons attest this, also. These skeletons are the Crane, the Starling, the Cormorant, and the Parrot, and in addition to these entire skeletons, there is the skull of a Woodpecker, showing the hyoid bone encircling the skull, and the tongue of a Parrot. In the drawing of the Cormorant skeleton Coiter shows the peculiar type of Cormorant foot with the webbing and tarsal sheath on one leg.

Chapter 2. De Differentiis Avium (Fig. 1). This cannot be called a classification in the modern, scientific sense of the word. We see it is a tabulation in outlined and bracketed form, and it presents at a glance a synopsis of Coiter's knowledge of birds, and shows that he had studied them both in the laboratory and in the field.

Space does not permit of speaking in any detail of this synopsis, but I would like to mention a few of his more discerning remarks, particularly those which indicate his having observed living birds in their natural habitats.

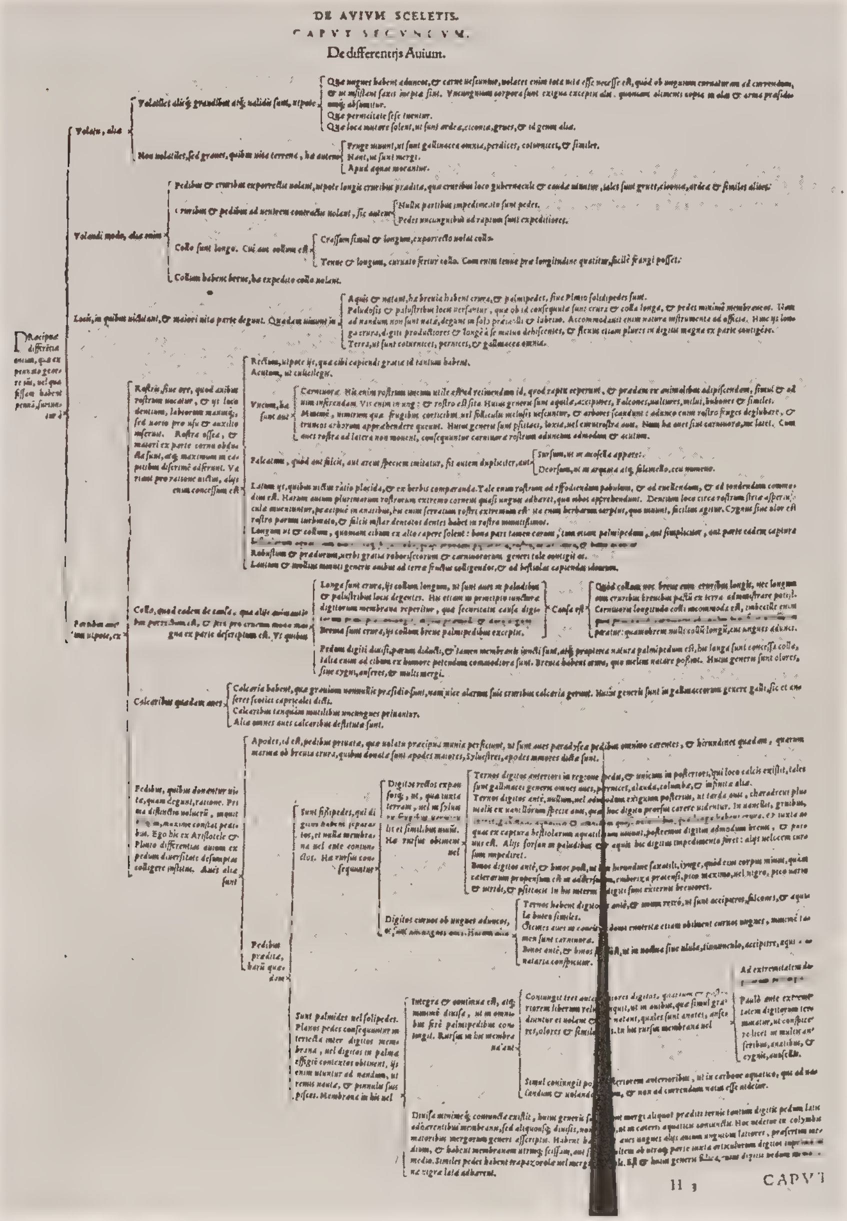
The author speaks of those birds which are wont to change their position, as are Herons, Cranes and Ibises. Coiter is referring to "mimicry", which many birds practice by making themselves resemble their immediate environment.

He speaks of birds with long legs, which they use as a rudder in flight.

Coiter speaks of the long, slender-necked birds, which fly with a fold in the neck, because a long, slender neck can be easily broken when shaken, if the neck be slender in proportion to its width.

As to his tabulation of environment, Coiter points out the adaptations of certain birds to their surroundings; for example, the Marsh birds, whose toes are elongated, but are only slightly webbed in order to fit them for walking in slippery, wet places.

As to the parts of birds, Coiter gives an outline of the different types of beaks and points out the kind of food suited to each — 1. the straight beak



DE AVIVM SCELETIS.

CAPVT SECVNDVM.

De differentijs Auium.

Fig. 1. Volcher Coiter's classification of birds in Chapter 2, »De Differentiis Avium«, in his work »De Avium Sceletis et Praecipuis musculis«, 1575. By courtesy of the Library of the Surgeon General, Washington D. C.

for seizing; 2. the hooked beak for tearing flesh; 3. the broad beak for those of placid habits like foraging in the grass; 4. beaks with saw-like edges in place of teeth, as in some ducks; 5. beaks that are neat and delicate for collecting vegetable matter and catching insects.

Coiter, likewise, takes up the necks of birds with a good deal of detail, and makes this generalization — "It is not possible for a bird with short neck with long legs nor a bird with long neck with short legs to manage feeding from the ground, and no bird with hooked claws has a long neck".

In his discussion of the feet of birds, Coiter departs from his own observation, and follows Pliny, thus falling into the error of thinking that certain birds are without feet. These he calls the Apodes, and assigns to this group the Birds of Paradise, which until modern times, were thought to be footless.

He recognizes that most birds have three toes in front and one behind, but makes the erroneous statement that the hind toe takes the place of a spur.

Some birds, Coiter says, have only three toes; and some have two toes directed forward and two backward, as in the parrots, and in their case, the inner toes are shorter than the outer.

Lastly, in his tabulation, Coiter takes up the flatfooted birds, by which odd term he seems to mean the seabirds, which rest on the whole tarsus, as the Auks and Murres; the different types of membrane or webbing between the toes, which may be whole, as in Ducks, divided as in some Gulls, or joined to the rear toe, as in the Cormorant or fluted, as in the Coot.

When we consider Coiter's dates of the mid-Sixteenth Century, when civilization was little directed toward the animate world, it is surprising that he knew so accurately the details of bird structure, and also so much of their life habits. It should be mentioned here that Coiter is the author of another ornithological treatise — the De Anatomia Avium, published in Nürnberg in 1573.

I am indebted to my friend, Mrs Elizabeth Van der Hoek, for translations of some Dutch articles on Coiter, from which I have extracted the following brief notes on his life.

Volcher Coter was born in Groningen, North Holland in 1534, the son of a lawyer, and left home at twenty-one to study abroad with the aid of a scholarship awarded to him in 1555 by the Town Council of Groningen.

Always interested in anatomy and surgery, he visited the medical center of Montpelier and came in 1559 to Bologna, where he was a fine student under Aldrovandus. At the latter's behest, Coiter carried on daily observations on chick embryos. When only thirty years of age, Coiter had risen to third in rank at the Great Italian University, but in 1556—7 his name disappears from the register. Apparently, others jealous of his success, plotted against him, and hampered his work. It is probable, too, that he became a follower of the Protestant, John Calvin, and for this reason was not tolerated in Italy.

From Bologna he went to Nürnberg, became the town physician and wrote his principal works. In 1576 he went with Johann Casimer, Count of the Palatinate, as Army Physician in the Huguenot Wars. He did not return from this expedition, but died, probably of leprosy, just as peace was declared in July, 1576.

When a thorough appraisal of Coiter's contribution to Ornithology is worked out, we shall owe him much honour for his pioneer studies of birds.

*Discussion:*

E. Stresemann drew attention to the fact that Coiter was the first taxonomist who based a system of birds on structure and not on function.

# Nomenclature in Guinea Fowls

*Alessandro Ghigi*

*Zoological Institute, Bologna*

Linnaeus called the guinea fowl *Phasianus meleagris* (Sist. Naturae Ed. X 1758, p. 159) and later (1766) he gave it the name of *Numida meleagris.* This latter name was retained for the strain living in a domesticated state and for its wild ancestors in Morocco and as far as the Gulf of Guinea, without any attempt at changing it, until 1919—a period of 161 years!

In 1919 Doctor Hartert (Bull. Brit. Orn. Club 39, 1919, p. 86) gave it once again the name of *galeata,* given to the bird by Pallas in 1767. The common guinea fowl is known by this name in the, *Systema avium aethyopicarum,* London, (Wheldon and Whesley, 1924, p. 95) edited by W. L. Sclater in collaboration with a special committee of the British-American Ornithologists' Union. The same nomenclature is adopted in Peters' catalogue, vol. II, published in 1934.

As early as 1930 I called the attention of the IX International Zoological Congress of Padua (1930) to this question of nomenclature and received a favourable opinion from the representatives of the Commission for Zoological Nomenclature of that time on the re-adoption of the name *Numida meleagris* instead of *Numida galeata* and of *Numida ptilorhyncha* instead of *Numida meleagris.*

I therefore adopted the old names in my book "Galline di Faraone e Tacchini" (Guinea fowls and Turkeys), Hoepli, Milano 1936. Critics who reviewed my book were surprised by the nomenclature which I had retained, evidently because they did not understand my reasons, which were written in Italian.

It is for this reason that I report the question to the present Congress in English, in order that I may be better understood.

Doctor Hartert had rightly remarked that it was not known precisely what the *Phasianus meleagris* of Linnaeus was; firstly, because his description makes no reference to the colouring of the caruncles; secondly, because he quotes Hasselquist who, in his ITER refers undoubtedly to the Eastern strain with blue caruncles; and finally because he also speaks of *Gallina guinea* and *guineensis,* geographical indications applicable to the Western strain.

*P. vertice calloso, temporibus carunculatis*
*Gallina vertice corneo.* Hasselqu. iter. 274.
*Gallus vertice corneo,* Sist. Nat. 28.
*Gallina guinea.* Worm. Mus. 297.
*Gallina africana.* Markgr. Bras. 78.
*Gallus niger, maculis ovalibus et erbiculatis.* Bar. Av. 79.
*Gallina guineensis.* Worm. Mus. p. 297 T. 297 Olear Mus. T. 15 f. 3 Raj. Av. 32 Alb. Av. 2. p. 32, T. 35, Will Orn. 162 p; 26. Aldr. Av. L. 14. C. 13.
*Habitat in Africa.*

But Linnaeus himself clarifies the question, when in his Editio Duodecima Reformata, of 1766, he adds: "*mansuescit*" *Caruncula maris coerulescens, feminae rubens.*

*Numida meleagris* L. 1766 is therefore the domestic strain and this name also belongs to the strain from which it is derived. The mistaken reference to a secondary sexual difference in the colour of the caruncle is mystifying, and we may suppose that Linnaeus had an Eastern male and a Western female. But it should also be noted that the flaps of the domestic guinea fowl are much larger than in the wild guinea fowl, being completely red and small in the females, while in the males they are considerably larger and the upper part is whitish like the face.

Hartert then, believing that the *Phasianus meleagris* of Linnaeus comprised the strain with red caruncles and that with blue caruncles, preferred to reserve the name *meleagris* for the Nubian strain. Having made this decision, Hartert states that since the name *meleagris* is no longer available, having been given to the Nubian strain, it is necessary to give another name to the Western domestic strain and that this name ought to be *Numida galeata* Pallas 1767.

The point at issue is precisely this: was Hartert right or not in preferring that the name *meleagris* should be applied to eastern *ptilorhyncha,* rather than to the domesticated western strain?

Hartert affirms that the *meleagris* of the Romans was, according to Columella, the strain with blue caruncles. Columella in fact says ("de re rustica, lib. VIII cap. 2): "The African (guinea fowl), called Numidian by the greater part (of scientists), is similar to the *meleagris* except that it has on its head a sandy-coloured helmet and crest, both of which are blue in the *meleagris*."

In the first place the change proposed by Hartert is not absolutely necessary in deference to the principle of priority. Since this applies from 1758 with reference to the tenth edition of Linnaeus' "Systema Naturae," the citations of Columella and Hasselquist have not a strictly judicial value: finding ourselves confronted with a Linnaean species that probably comprises two, it remains to be decided which of these is to retain the name given by Linnaeus. Hartert preferred to deprive the domestic strain of the name that it had borne for 161 years to bestow it on the Nubian species.

However, in 1766, Linnaeus makes clear with his "*mansuescit*" that his *Numida meleagris* is the domestic strain, and Linnaeus' name has precedence over the name *galeata* given to it by Pallas in 1767.

The guinea fowl is a common domestic bird. Farmers and breeders are interested in it; all the natural history books in the secondary schools discuss it, and everybody has always called it and continues to call it *Numida meleagris*, meaning by this name the domestic strain and its wild ancestors with red caruncles of West Africa.

If the retention of the name *meleagris* for the common guinea fowl corresponds simply to criteria of opportunism, the attribution of this name to the Nubian strain, known by the name of *ptilorhyncha* Less, produces a deplorable confusion in a scientific field not less important than that of classification, I refer to the genetic field.

Darwin, discussing the variations in domestic animals and plants, made the mistake of admitting the descent of the domestic guinea fowl from *Numida ptilorhyncha*, that is to say from the Nubian strain with blue caruncles. This error in genetics, given the great authority of Darwin, has been repeated in numerous books. To attribute the name of *meleagris* to the Nubian strain now will intensify the diffusion of an error in genetics; the error, that is, of holding that the domestic guinea fowl is derived from the Eastern progenitor, not domesticated nor capable of being domesticated, instead of from the Western progenitor, capable of being domesticated and domesticated.

Hartert wrote that the numidic fowl with red caruncles, known by the Romans, must have been the strain that lives at present in Morocco and that he at first called *Numida sabyi* and subsequently *Numida meleagris sabyi*. This Moroccan strain belongs without doubt to the group *meleagris* with red caruncles, but in the name given to it by Hartert the expression *meleagris* refers, on the contrary, to the *ptilorhyncha*, or to a strain from which the sabyi is clearly distinct both morphologically and geographically.

However, if we wish to leave aside modern rules of zoological classification and we ask ourselves what the *meleagris* of the ancients was, we have to reply that this was the Western strain with red caruncles and that Columella was mistaken in his definition. Apart from the fact that Columella is certainly not the most highly esteemed among the Latin naturalists as far as birds are concerned, the question was resolved by Atheneus of Naucratis in Egypt (Columella was born at Cadiz in Spain), who, quoting a passage by Clitus of Miletus (Book XIV 655 A) a disciple of Aristotele, writes as follows:—

"In the temple of Minerva at Leros there are birds called *meleagris*. The land on which they feed is marshy. This bird does not love its young; it neglects them, so that it is necessary for the priests to take care of them. Its size is that of a vigorous strain of hen; its head is small in proportion to its body and is bald; it has a horny rigid crest, the colour of wood, which looks like the round head of a nail. Along its cheeks there are, like a beard, two pieces of hanging flesh, redder than in the hen, but there is not that crest which is found on the beak of the hen; this is a part which seems to be lacking. Its beak is black, bigger and shorter than that of the hen. The whole of its body is spotted on a black background and there are innumerable spots larger than lentils; they are small circles among black lozenges, the entire plumage is patterned in this manner, the black sprinkled with white, and the white on a black background. The wings are traversed with white stripes set like the teeth of a saw, or small flames parallel to one another. These birds have no spurs in their talons and in this respect they resemble hens. The female is more or less like the male, so that it is difficult to distinguish them."

It is clear that the only full and exact description of the *meleagris* of the Greeks refers to the strain with red caruncles of West Africa, known by those geographers who have given an exact description of the locality.

A passage from Plinius (XXXVII, II) is very important from the zoogeographical point of view:

"Asaruba says that along the Atlantic sea-board there is a lake Cephisis, called Electron by the Mauri; this lake, heated by the sun, produces floating amber from the slime. Mnasea calls this locality of Africa Sicyon, and Crathis the sluice which carries the waters of the lake to the ocean; in the lake lives the bird that he calls Meleagris and Penelops; here it is born in the same manner as was described before."

Where the lake Cephisis was, the geographer Scylax Caryandeus (Periplus, 12) tells us:

"Who sails beyond Hercule's Columns towards the outer sea, with Africa on his left, comes to a large bay, which extends to the promontory Ermeus (here too there is a promontory Ermeus). In the middle of the bay is the country and town of the Pontii. In the vicinity of the town there is a large lake, and in this lake there are several islands. Around the lake grow reeds, cyperi, stebi (marsh weeds) and bulrushes. Here are the birds Meleagrides, which are not to be found anywhere else unless they have been transported from here. This marsh is called Cephisis and the bay Cote; and is half-way between Hercule's Columns and the promontory Ermeus."

It appears to me that from what I have said there emerges the justification for referring the name *Numida meleagris meleagris* Linnaeus to the Western strain, at present designated in the catalogues as *Numida meleagris galeata* Pallas and for re-applying the name *Numida meleagris ptilorhyncha* to the strain of Abyssinia and Nubia.

I beg the X International Ornithological Congress to put the decision resulting from this enquiry before the International Commission for Zoological Nomenclature.

# A Nomenclatorial Controversy:
# The Genus Colymbus Linnaeus 1758

*Finn Salomonsen*

*Zoological Museum, Copenhagen*

For more than seventy years ornithologists of the Old and the New World have differed in their use of the generic name *Colymbus* of Linnaeus 1758 (Syst. Nat., ed. 10, I, p. 135). In North and South America *Colymbus* is the name of the Grebes while the Divers or Loons are called *Gavia* Forster. In the Old World, including Europe, Asia, Africa and Australia, *Colymbus* is the name of the Divers while the Grebes are called *Podiceps* Latham. Not only has the generic name *Colymbus* a different meaning in the two hemispheres of the world, but also—as a consequence of this—the family *Colymbidae* and the order *Colymbi* have become the designation of two widely differing groups of birds. This awkward situation cannot continue. I suggest that measures should be taken by this Congress to put an end to the controversy. The fatal point, which has given rise to the disagreement, is the uncertainty which is attached to the designation of the type-species of the genus *Colymbus*. The regrettable fact is that all subsequent designations of a type-species of this genus are indistinct or obscure and may in one way or another be subjected to criticism.

The history of the genus *Colymbus* has been discussed over and over again in literature, but nevertheless I think it necessary to give a brief outline here. Firstly the rather astonishing fact must be mentioned that there are two genera *Colymbus*, one of Linnaeus 1758 and one of Moehring 1752 (Av. Gen. 77, p. 34). This latter name, having been published earlier than 1758, has no standing in nomenclature. Brisson in 1760 (Ornith. 6, p. 34) has chosen a Grebe (*C. cristatus*), not a Diver, as the type-species of *Colymbus*, but he divided the genus *Colymbus* of Moehring, not that of Linnaeus, as recently pointed out by Grant (The Ibis 90, 1948, p. 330). Being pre-1758 this name is unacceptable, and besides—if Brisson's name was acceptable—it would be preoccupied by *Colymbus* of Linnaeus 1758. Reichenbach in 1852 (Avium Syst. Nat., Gattungsliste, p. III) chose a type-species of

"*Colymbus* Brisson" and thus—although indirectly—based his type on the genus of Moehring.

The Linnean genus was first divided by Latham in 1787 (Gen. Synops. Suppl. I, p. 294). He separated two groups, the Grebes, for which he used the name *Podiceps*, and the Divers, for which he retained the name *Colymbus*. This division was quite clear and convincing and could not be misunderstood. It was accepted by all ornithologists for almost a hundred years, right up to 1882, when Stejneger (Proc. U. S. Nat. Mus. 5, p. 42) abandoned the well-established system and in this way started the unfortunate and unnecessary development, which separated ornithologists of the New and the Old World. According to the recommendation c to article 28 of the *régles*, the name to be preferred as a type-species is placed first in the publication, other things being equal. Unfortunately Latham's first species was *Colymbus glacialis* (= *C. immer* Brünnich 1764), a bird which was not mentioned by Linnaeus in the original description of *Colymbus* in 1758, but was included in his list of 1766 (Syst. Nat., ed. 12, I p. 221), where the genus in question was augmented with many more species than in 1758. What concerns us, however, is not the genus *Colymbus* of 1766 but that of 1758. According to article 30, II, e, alpha of the *régles*, a type-species cannot be a species which is not mentioned in the original description. Therefore it is wrong to maintain *C. glacialis* as the type-species according to Latham, although this has been done by several authors, for instance by Grant (*l. c.*). The only species common to *Colymbus* of Linnaeus 1758 and that of Latham 1787 is *C. arcticus*, and this species has, therefore, been chosen as type-species by Lönnberg (The Ibis 1927, p. 524). His procedure is thus based on elimination, a method no longer employed in nomenclature, and is further contradictory to the recommendation added to article 28 of the *régles*, mentioned above.

The next attempt at choosing a type-species of *Colymbus* was made by Gray in 1855 (Cat. Gen. Subgen. Birds, p. 125), but the unlucky genus was again followed by misfortune. Gray writes "*Colymbus* Linn. 1735 nec 1766, Type *arcticus*." The reason for writing "nec 1766," as shown by Sclater (The Ibis 1928, p. 819) was that Linnaeus in his twelfth edition added the species *grylle* and *troille* to the genus *Colymbus* and placed them first. Gray thus chose a type-species of *Colymbus* Linnaeus 1735 and did not mention the edition of 1758 and this—from a strictly formal point of view— made the designation valueless (cf. also Stone, The Auk 1923, p. 147; Wetmore, Bull. U. S. Nat. Mus. 133, 1926, p. 45; Laubmann, Wissensch. Ergebn. deutsch. Gran Chaco-Exped. 1930, p. 46, foot-note 4).

A few years later than Gray, Fitzinger (Sitzungsber. Akad. Wissensch. Wien, Math.-Naturwiss. Kl., 51, 1865, p. 320) chose *C. arcticus* as the type-species of *Colymbus*, but he did not do it in a formally correct way. Hellmayr & Conover (Field Mus. of Nat. Hist., Zool. Ser. 13, part 1, No. 2, 1948, p. 18, foot-note) have pointed out that Fitzinger in his preface explains that he intended to give "eine Aufzählung sämmtlicher Gattungen und Untergattungen, unter Angabe einer ihrer typischen Arten" (*one* of the typical species), a statement which does not seem to be in conformity with the international rules.

American ornithologists often credit Baird, Brewer & Ridgway (Water Birds of N. Am. 2, 1884, p. 425) for having chosen *C. cristatus* as a type-species of *Colymbus*, but—like Lönnberg—these authors used the method of elimination, an action that must be considered invalid under present rules.[1] Nevertheless, the "Check-list of North American Birds," ed. 3, 1910, p. 21, gave *C. cristatus* as type-species "by subsequent designation."

It is obvious that the authors in the old days, when no nomenclatorial codes or rules were invented, agreed in considering *Colymbus* as a genus of Divers, not of Grebes, with or without knowledge of Latham's paper of 1787. For more than a hundred years *Colymbus* was the name of the Divers, *Podiceps* that of the Grebes, and no one argued about this division, Latham's restriction of *Colymbus* to the Divers being quite clear. In spite of the insufficient designation of the type-species, the use of *Colymbus* as the name of the Divers ought to have been continued. In my opinion American ornithologists committed a serious blunder when they mixed up the Linnean genus with *Colymbus* of Moehring-Brisson and chose a Grebe as type-species.

The disagreement between the American and the Old World opinion as to the interpretation of the genus *Colymbus* has been an intolerable drawback for a long time. About 1925 the American ornithologist Dr. Witmer Stone requested the opinion of the International Commission on Zoological Nomenclature in regard to the type of *Colymbus*, and he was in agreement with his countrymen in considering the selection made by Baird, Brewer and Ridgway in 1884, of *C. cristatus* as the type-species, to be the final one. On behalf of the European ornithologists, W. L. Sclater prepared a memorandum (published in The Ibis 1928, p. 818) and submitted it to the International Commission. He suggested that the designation made by Gray in 1855 of *C. glacialis* as the type-species should be accepted. Unfortunately the Commission was unable to reach an unanimous decision. Still in 1936 Hartert & Steinbacher (Vögel d. pal. Fauna, Ergänz. Bd., Heft 5, nov. 1936, p. 453) were sorry to admit that "die Meinungsverschiedenheit, welche zwischen den amerikanischen und den europäischen Systematikern über den Typus von *Colymbus* besteht, hat sich immer noch nicht überbrücken lassen." In the 25 years, which have passed since Witmer Stone and Sclater requested the opinion of the International Commission, nothing has happened. As recently as 1948 two papers were published on the subject in question. The Americans Ch. E. Hellmayr & B. Conover (*l. c.*) created a new type-species of *Colymbus*, choosing "by present designation" *C. cristatus*, and the European ornithologist C. H. B. Grant (*l. c.*) was of the opinion that "we should accept *Colymbus glacialis* Linnaeus as the genotype of the genus *Colymbus*," based on Latham. In the new edition of the Check-list of Birds of Japan (1942) *C. immer* is chosen as the type-species of *Colymbus*. This shows that we are to-day as far from each other as ever before. We cannot continue like this. It is ridiculous and intolerable that Grebes and Divers, such widespread and well-known birds in the northern hemisphere can never be called by their scientific designation, but must be indicated by local, vernacular names. What must we do? How can we put an end to the state of confusion?

---

[1] Baird, Brewer & Ridgway quote Sundevall (Met. Av. Nat. 1872, p. XXIX), saying that he has shown that *Colymbus* should never have been retained for the Divers. Sundevall, however, only gives some historical comments of no nomenclatorial significance.

I consider that the time is long past when a purely juridical solution would suffice to restore uniformity in the nomenclature of the Grebes and Divers, for whatever form that solution took, it would be inevitable that the name *Colymbus* would apply to one or other of these groups of birds, a result which would do little to improve the present situation in view of the confusion which, after so many years of conflicting usage, must always be involved in the use of this generic name. Fortunately a purely juridical solution is not the only one which it is possible to seek, for the International Commission on Zoological Nomenclature has been endowed by the International Congress of Zoology with plenary powers to suspend the normal operation of the Code, where, in its opinion, confusion would otherwise arise and where, therefore, such action is necessary to secure stability in nomenclatorial practice. It is a solution of this type which I recommend that ornithologists should seek.

The fact that for such a long time *Colymbus* has been—and still is—used in a totally different way in the New and the Old World had, in my opinion, compromised the name *Colymbus* in a hopeless manner. It would have too far-reaching consequences to accept a solution which in a one-sided way favoured one part at the expense of the other. Each part has to make a sacrifice, and this may be accomplished by giving up the name *Colymbus* altogether, and proposing the name *Podiceps* Latham 1787 and *Gavia* Forster 1788 as *nomina conservanda* for the Grebes and the Divers, respectively. By this procedure the European ornithologists must change the name of the Divers from *Colymbus* to *Gavia*, and the American ornithologists that of the Grebes from *Colymbus* to *Podiceps.*

At the meeting of the International Commission on Zoological Nomenclature during the International Zoological Congress in Paris 1948 the *Colymbus* question was discussed and it was decided to attempt to solve this intricate problem, one of the most important items among the still unsolved questions in zoological nomenclature. I have contacted Mr. Francis Hemming, secretary of the International Commission on Zoological Nomenclature, and Dr. Henning Lemche, member of the Commission. Mr. Hemming informs me that the Commission would gladly take, as the basis of its further consideration of this case, any authoritative pronouncement of the wishes of ornithologists that might be submitted to it. Mr. Hemming added that it was not to be doubted that the Commission would give the most sympathetic consideration to any proposal, which might be received that had the backing of leading ornithologists on both sides of the Atlantic.

Clearly, no gathering could speak with greater authority on this subject than the present Congress, including, as it does, among its members the leading ornithological authorities of the world. It is also particularly fortunate that the Commission itself is anxious to secure a satisfactory solution of this longstanding difficulty, for it gives the present Congress an unique opportunity for devising a settlement agreeable to the largest possible number of ornithologists in all parts of the world. It is for this reason that I now seek from the members of the present Congress an expression of their views as to the best method to be adopted for putting an end to the confusion, in which the nomenclature of the Grebes and Divers has been involved for such a long time.

If, as I hope, the views which I have expressed command the approval and support of the majority of ornithologists present, I suggest that the Congress should adopt a resolution that a proposal in the following terms be submitted to the International Commission on Zoological Nomenclature:—

> The undersigned ornithologists assembled at the International Ornithological Congress at Uppsala, June 1950, being deeply impressed with the need for putting an immediate end to the confusion in ornithological nomenclature which has long existed owing to the lack of agreement regarding the type species of the genus *Colymbus* Linnaeus, 1758 (*Syst. Nat.* (ed. 10) 1: 135) submit the following application to the International Commission on Zoological Nomenclature, namely that the Commission should:—

(1) use its plenary powers:—

- (a) to suppress the generic name *Colymbus* Linnaeus, 1758, for the purposes of Article 25 but not for those of Article 34;
- (b) to set aside all type selections hitherto made for the undermentioned genera and to designate as their respective type species the species specified below:—

| Name of genus | Species designated as type species |
|---|---|
| *Gavia* Forster, 1788, *Enchiridion Hist. nat.*: 38 | *Colymbus immer* Brünnich, 1764, *Orn. boreal.*: 38 |
| *Podiceps* Latham, 1787, *Gen. Synopsis* Birds, Suppl. 1: 294 | *Colymbus cristatus* Linnaeus, 1758, *Syst. Nat.* (ed. 10) 1: 135 |

(2) to place on the "Official List of Generic Names in Zoology" the generic names *Gavia* Forster, 1788, and *Podiceps* Latham, 1787, with, as their respective type species, the species so designated under (1) above;

(3) to place the undermentioned trivial names on the "Official List of Specific Trivial Names in Zoology":—
*cristatus* Linnaeus, 1758 (as published in the binominal combination *Colymbus cristatus*);
*immer* Brünnich, 1764 (as published in the binominal combination *Colymbus immer*);

(4) to place the generic name *Colymbus* Linnaeus, 1758, on the "Official Index of Rejected and Invalid Generic Names in Zoology."

*Post Scriptum by the General Secretary.* In order to discuss the foregoing motion a special meeting was arranged, to which all members of the Congress interested in the subject were invited. At this meeting a special committee was formed with the aim of stabilizing the ornithological nomenclature, especially by introducing *nomina conservanda* in particularly intricate cases. Prof. J. Berlioz, Colonel R. Meinertzhagen, Prof. E. Stresemann and Dr. J. Zimmer were elected as members of this Committee of Ornithological Nomenclature. The Committee has been endowed by the International Ornithological Congress with the power to submit to the International Commission on Zoological Nomenclature any proposal for establishing *nomina conservanda,* which are necessary in order to stabilize ornithological nomenclature. The foregoing motion concerning the generic name *Colymbus* was handed to the Committee for further consideration.

# Desert Colouration

*R. Meinertzhagen*

*London*

So many false impressions are derived from careful records of perfectly true facts. I hope to give you the facts as I know them, having studied life in every absolute desert in the world except the Gobi; my interpretation of these facts may, or may not, be correct and in any case I do not claim to have solved the question of Desert Colouration: I merely offer a suggestion.

Gloger's well-known Rule lays down that increased humidity involves increased pigmentation in plumage and that more arid conditions entail a decrease in pigmentation. This rule holds good in the majority of cases but there are many exceptions. The Skylark (*Alauda arvensis*) is one of the best examples of the rule. It inhabits the whole of the Palaearctic Region from Ireland to Japan and south to Ceylon. In the most arid part of its range the palest race occurs—in East Persia and Central Asia—and from those areas there is a perfect colour-cline radiating out to West Ireland in the West and Japan in the East and Ceylon in the South, these three latter areas having the darkest races. But there are many exceptions to Gloger's Rule. I shall quote two only. In Arabia there live two races of *Ammomanes deserti*, the one almost black on black lava desert and the other a very pale sandy colour on pale sand. They live within a few miles of each other under similar climatic conditions: the second exception is of a different type: in the British Islands most recognisable races tend to be darker than continental ones and show agreement with Gloger's Rule; but coastal sea-birds living in even more humid conditions tend to be paler than their continental representatives—Herring Gull, Lesser Black-backed Gull, Guillemot, Razorbill.

Gloger's Rule has often been associated with camouflage and cryptic colouration. I believe such association to be false.

Gloger's Rule has also been associated with selection; that also I believe to be false; in the British Islands we have the resident dark races of Skylark and Song Thrush but in winter we have vast numbers of the paler continental Skylarks and Song Thrushes living alongside the dark birds for seven months of the year and not suffering a disadvantage due to colour which is scarcely perceptible in the field.

In deserts we find an almost universal tendency towards 'desert colouration' among birds. This colour is a pale, rather red, sandy-isabelline, closely resembling the colour of the desert and this has led to the belief that desert colouration has selective value against predators, offering to desert birds a cryptic colouration as camouflage.

I now wish to make some remarks on various aspects of Camouflage and cryptic colouration.

### *The Widespread Nature of Camouflage*

Cott's "Adaptive Colouration in Animals" leaves no doubt on the widespread nature of Camouflage throughout the animal kingdom, but it is patchy and not universal.

The best and most usual form of camouflage is the elimination of shadow and avoiding movement. The best camouflage is destroyed by movement.

There is, however, one aspect of camouflage which transforms movement into camouflage. Birds whose normal habitat is by streams of running water are not only spangled like spray but keep their tails or heads in constant movement in rhythm to rushing water; such birds are the Grey Wagtail (*Motacilla cinerea*), *Enicurus*, the Terek and Common Sandpipers (*Xenus* and *Tringa hypoleuca*), *Mergonetta* and *Cinclus*, and many of the fish-eating *Alcedinidae*.

The next best form of camouflage is cryptic colouration, either close resemblance to environment or close resemblance to some object which does not interest predators.

### *The Awareness of Camouflage*

How far are birds aware of their cryptic colouration? There is no doubt that some birds cryptically coloured make full use of the deception but I have seen many exceptions. A Bittern in its reed-like attitude is difficult to see in reeds; but I have seen them employ that attitude when surprised in the open where no amount of reed-like posture would make them anything but conspicuous. Parrots and Green Pigeon (*Treron*), whose habit is to "freeze" if surprised feeding in a tree, so as to become invisible in green foliage, will "freeze" equally well in a tree bare of foliage under the impression that they are invisible, when, in fact, they are very conspicuous. Again, there is a black lizard living on black lava in Arabia. On black rocks he is invisible. But alongside a recent road made through this black lava, the larger boulders have been white-washed to mark the road; these lizards will often take refuge, if disturbed, on these white rocks under the impression that they are hidden. Again, small flocks of Sandgrouse, if approached on open desert where they would be invisible if they remained still, will waddle along, neutralising the camouflage they possess. My experience of desert birds is that they very seldom crouch and make full use of their cryptic colour; they are constantly on the move, restless and are more apt to sit upright, run or hop on to a stone, than squat or crouch. Even should a hawk pass their way, they prefer to fly than crouch.

In this respect they behave very differently to non-desert birds in grass or bush country who squat or take refuge in a bush if a hawk comes into sight.

### *Reality of Camouflage*

Desert colouration is a perfect camouflage if the bird remains still. So perfect is it, that if one shoots a bird and it falls back-up, it may take a long time to find it. On one occasion in the Namib Desert of South Africa, three of us were unable to find a large Bustard for a considerable time though it fell in country devoid of any sort of cover; and it was not until one of us trod on it that we found it.

But perhaps the best example of perfect camouflage is to be found in the Lark—*Ammomanes deserti.* This species is divided up into many races, all preferring rather rocky country and in every known race the colour of the plumage exactly matches the colour of the rocks among which the race lives. In one case, the darkest race (*A. d. annae*) living on black lava desert, has a contiguous distribution with one of the palest races (*A. d. coxi*) living on pale yellow desert. Neither race can be induced to leave their own particular coloured environment. The question of climatic influence cannot arise, for both races live in similar climatic conditions. But this lark makes no use of its cryptic colouration, never crouches but stands upright, always on the move and, in fact, invites attention. And though comparatively conspicuous in life, owing to movement, once dead and still, one has the utmost difficulty in finding them. On two occasions I have seen migrating Harriers pass over dead Ammomanes without locating them.

I placed the dead birds, back uppermost, on specimens of the rock on which they lived, in a wadi bed up which Harriers were migrating. They were not located by two Harriers. I then removed the birds to yellow sand where they were at once pounced on by the first Harrier which passed.

### Unnecessary Camouflage

There are many cases of birds and mammals having desert colouration when it can have no value in respect of survival from predators. The desert Eagle Owl (*Bubo desertorum*) and the desert race of the Barn Owl (*Tyto alba erlangeri*) are perfect examples of desert colouration but they are both nocturnal hunters, making their cryptic colouration meaningless. There are also Swifts (*Apus melba marjoriae*) of South West Africa, and Martins (*Riparia obsoleta arabica*) which conform to desert colouration but which have no possible cryptic explanation; the Peregrine Falcon of desert areas has assumed a pale blue-grey mantle which can be of no use to him as a survival factor. Desert colouration extends to Bats, Rodents living by day under ground and to *Spalax* which never sees the light of day.

There are also cases among birds where the female is cryptically coloured and the male conspicuous, especially in *Oenanthe*—the Chats. This would make sense if the female incubated her eggs in the open, but the nest is always concealed under stones or in a rodent burrow.

### The Necessity for Camouflage in the Desert

Have desert birds any need for camouflage against predators? My own observations go to show that they have not this need nor do they take advantage of their cryptic coloration. The Sparrowhawk *Accipiter* family is the small bird's most dangerous enemy, but I have never, during many months spent in desert lands, seen a Sparrowhawk hunting in the desert. Nor have I seen the small falcons—Hobbies, Merlins etc.—in the desert. One occasionally sees a Kestrel, but these are hunting for lizards, grasshoppers etc, and small rodents. I have never observed a Kestrel take any interest in a desert bird nor a desert bird take any interest in a Kestrel. Birds know their hawks. They know that by flying they are safe from harriers, *Melierax* and eagles; they know they are safe on the ground from the larger falcons and Sparrowhawks. Niethammer ('Birds S.W. Africa' 1940: 82–3) is of much the same opinion.

But there is a significant fact in connection with camouflage which must be recorded. Birds which usually live on the ground—Larks, Pipits, Sandgrouse and the *Galliformes*, tend to develop a greater degree of cryptic colouration than those birds which do not live on the ground; and the greater the absence of cover, the more highly developed becomes cryptic colouration.

### *Exceptions to Camouflage*

Colours in plumage can be roughly classified as pigmentary and refractive. The latter which one finds in Grackles (*Onycognatus*), Ravens (*Corvus corax*), Starlings (*Sturnus vulgaris*) and in Chats—for example *Oenanthe leucopyga*—does not respond to desert conditions, though the desert Raven (*Corvus corax ruficollis*) does its best in having a copper coloured nape and mantle in fresh plumage. Blacks and whites appear to be resistant to desert colouration. It is the browns and yellows which respond. Dark browns are entirely absent from desert birds and so are mottled upperparts.

There are several species of black and white Chats (*Oenanthe*) in the desert, sometimes most conspicuous—but they appear to be just as successful in competition against predators as other birds in desert conditions. But in S.W. Africa we find the Snowy Chat (*O. albicans*) which has assumed cryptic colouration yet cancels it out by being most active and preferring to advertise himself from a bush than to use his perfect camouflage. It is noteworthy that the Chats have not a high value in edibility, a fact which Cott has proved and which I can confirm.

All those birds which show exception to desert colouration belong to species which can and do take advantage of shade in or under bushes during the midday sun.

Recently in S.W. Africa I came across a curious paradox in cryptic and non-cryptic colouration. Two Bustards—*Afrotis afra* and *Eupodotis rüppelli* —live more or less together in thin bush and more or less open country with much grass respectively. *Afrotis* is conspicuous black and white whilst *Eupodotis* is cryptically coloured. When *Afrotis* is alarmed, and he seems to enjoy the thrill of danger, he jumps on to a stone or mound, advertising himself as best he can, and when he flies he goes off with a loud cackle, dangling his legs and ruffling out his head and neck feathers, doing his best to attract attention despite his gorgeous plumage. But *Eupodotis,* if disturbed, either lies down (if in cover) or runs in a crouching attitude, and when he flies he rises without noise and goes a long distance. *Afrotis* seldom travels more than a few hundred yards.

We ate both *Afrotis* and *Eupodotis.* The latter was just edible, but the former can only be described as disgusting.

It is possible that edibility may account for the immunity of some conspicuous desert birds: a few simple experiments carried out with chats and larks in S.W. Africa certainly confirmed Cott's theory.

An interesting digression from normal is shown in the Egyptian Plover (*Pluvianus*). This bird lives in one of the hottest parts of the world, on open sand where the heat is intense. It is the only hot climate bird I know, living in open glare and heat and on the ground, which has no resistant colour in its plumage and has a pure white undercoat. But to compensate for this, it has a perfect black spine-pad, very similar to the spine-pad which Europeans in the tropics used to wear as protection against the sun a century ago.

To sum up, these examples and aspects of camouflage rather destroy the belief that desert colouration is of selective value against predators; desert birds enjoying cryptic colouration do not make use of it nor is there any necessity for them to use it; desert colouration must have a different interpretation to the cryptic colouration of birds living in bush, forest and grass where the danger from predators is of daily occurrence. Finally, many desert animals which have no need of desert colouration, by reason of their nocturnal or underground habits, react just as strongly to the desert as diurnal and surface-living animals. One must therefore find some other explanation than protective colouration against predators.

I have searched literature in vain for a satisfactory explanation. Buxton in his Animal Life in Deserts has given many facts but few convincing reasons. He does, however, suggest that desert paleness may be due to a combined effect of soil and climate; which is but another way of expressing an old truth that animal life fits its surroundings

Sumner, who has studied this question in connection with small rodents shows that there is a correlation between coat colour and the prevailing colour of the surroundings, but leaves us in doubt as to the cause. Mayr has suggested that some obstruse gland may be responsible. Stresemann has suggested a physiological reason, that birds of certain colours have a preference for soils matching their plumage. It is known that birds have a keen sense of colour and have colour preferences.

I think we have most of the facts, every one of which has many exceptions; and we have a great many theories, none of which fit all the facts. To paraphrase a remark on Soviet Russia—There is no expert on Desert Colouration; only varying degrees of ignorance.

The common factors of all deserts at some time of the year are, a strong sun, intense heat and glare, a low degree of humidity, the absence of shade and frequency of dust storms, combined with a general uniformity of the colour of the sand and sand-covered soil, as opposed to the variable colour of rocks or cultivated lands. I have also noted that the hotter the desert, the more does pigmentation react to desert colouration. There is a greater tendency towards desert colouration in the Sahara, Arabia and the Namib of S.W. Africa than there is in Arizona or the Gobi.

This led me to examine whether these facts might be responsible for desert colouration.

I can now return to facts. A curious pinkish-buff colour occurs at the bases of the feathers of desert Bustard, of Sandgrouse and certain species of Larks. This colour is strongly resistant to the rays of the sun and only occurs among birds which are exposed to a strong sun every day of their lives.

The body temperature of a bird is as vital to its existence as it is to man or any other animal. It must be maintained at a uniform degree. Its feathers in both texture and colour must be able to resist harmful rays of the sun.

Skin temperature, on which depends energy and good health, is to a large extent dependent upon the amount of sunlight, *i. e.* radiant energy absorbed. The colour of any object, whether animate or inanimate, determines the amount of sunlight which it absorbs or reflects, and this in turn determines the temperature of the object. Black absorbs and white reflects. A white shirt reflects 71 per cent of all sunlight, khaki cotton reflects 52 per cent, and black cloth reflects only 5 per cent. The skin of a European reflects from 45 to 35 per cent and the African about 16 per cent.

All African antelope which live entirely in the open have reddish coats, the forms living in arid areas having more grey and less red, whilst purely desert antelopes tend to be purely desert-coloured, slightly more red than the usual desert coloration of birds.

Among domestic cattle the light-coloured animals have more stamina than the dark-reds and blacks. Jersey cattle are one of the hardiest breeds in tropical climates, having a greater resistance to high temperatures by reason of their colour, which almost exactly resembles desert coloration. They have been developed in a warm mild climate and are on the small side therefore having a large skin surface per unit of weight. This breed also has a high percentage of carotin pigment in the skin which is a valuable protective pigment against intense solar radiation.

Therefore, in the case of animals with lighter coloured coats, the colour is a factor contributing towards keeping the animal's skin cool and in better health than those animals with darker coats.

Several writers have observed that among domestic animals developed in tropical and subtropical areas or adapted to such regions, light colour tends to predominate—pale reds, yellows and whites. Also that in hot climates, light coloured animals have more stamina than dark red or black animals.

### *Explanation of desert colouration*

I know of no satisfactory solution which solves the many complex problems and the many exceptions relating to desert colouration. The big exception is that of *Ammomanes deserti* which, instead of assuming desert colouration, reacts to the colour of its environment.

This may be accounted for by psychological selection, individual variation in plumage being linked with individual soil preference, thus the dark-backed *Ammomanes deserti* found dark soil more attractive and pale-backed larks found pale soil more attractive. Something of this nature has been suggested by those who have studied the colour phases of locusts in relation to the colour of the soil.

But solutions which do not fit the facts must be unsatisfactory.

I believe the Jersey cow may give us a clue to desert colouration, which, I suggest, has been evolved by selection of those birds whose mantle colour is best able to resist heat and glare and the black-and-white exceptions can be explained by the fact that both black and white, by absorption or reflection, are not quite-so-good protective agents, and that these black-and-white exceptions always occur where slight shade is available. A purely desert-coloured bird never, to my knowledge, takes advantage of even slight shade in the burning heat of a desert summer.

There is also the edibility aspect; in almost every tested case where a desert bird is conspicuous, edibility value is low.

The problem is not solved and I can only claim to have made a small contribution, in the nature of a suggestion, to a most complex subject.

# Adaptive Differences between Two Sympatric Species of Nuthatches (Sitta)

*Charles Vaurie*

*American Museum of Natural History, New York*

For the last two years I have been engaged in the study of the very large bird collections made by Dr. Walter Koelz in Iran, Afghanistan, and India. Four papers on passerine families have been published and three more are in press. These papers deal almost solely with systematics. Occasionally, however, challenging ecological situations were met. These situations concern very closely related species which were found to breed side by side. These species keep distinct, and, apparently, breed with equal success. This ecological problem, which has been discussed in detail by David Lack (1944, Ibis, pp. 260–286), throws a considerable amount of light on some aspects of species formation. In this paper I have singled the most striking case which has come to my attention. The case of the two rock nuthatches, *Sitta neumayer* and *Sitta tephronota.*

Before presenting my data, the ecological implications may be briefly reviewed. When two forms come to occupy successfully the same habitat in the same region, they must be separate species adapted to the taking of different foods. David Lack has suggested that these species originated in geographical isolation during which reproductive isolation and ecological compatibility were acquired. After they meet the adaptive characters become further intensified to minimize competition. In some of these cases, as shown by Lack, one species is larger than the other, in others there may be a conspicuous difference in the size of the feeding organ, the beak. In the case of the two nuthatches both of these requirements are met to a high degree.

(Fig. 1). The present range suggests that these two species were originally separated geographically and later came together. *Sitta neumayer* is a western species the range of which extends from Dalmatia eastward to certain parts of Iran. *Sitta tephronota* is an eastern species the range of which extends westward to Transcaucasia, Armenia, and northern Iraq. Thus, in Iran, certainly, and perhaps over the borders of western Iran the two species overlap broadly. In Iran, the region covered by my studies, the

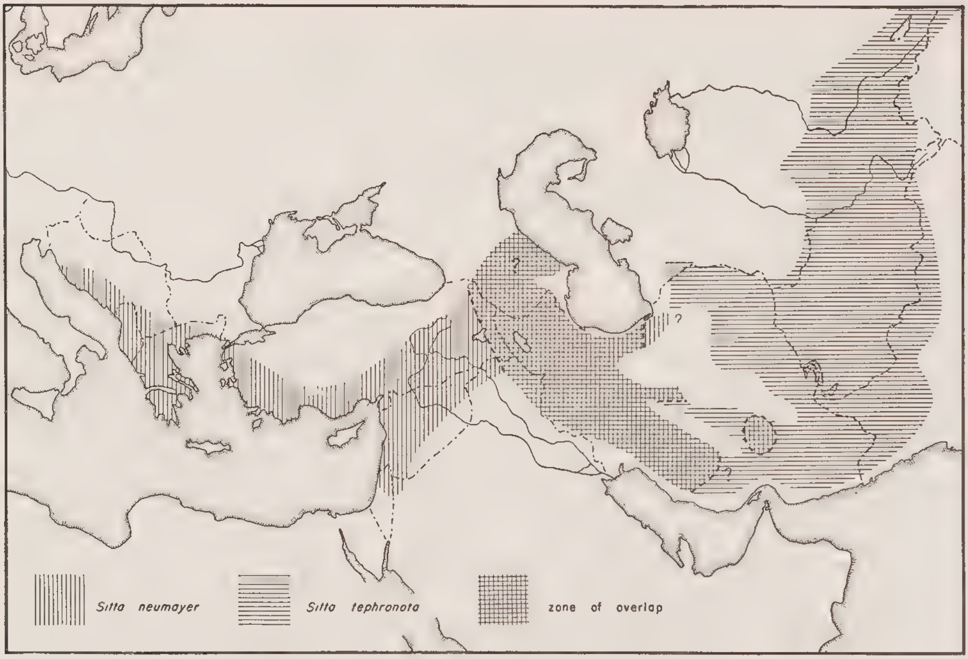


Fig. 1. Distribution of *Sitta neumayer* and *S. tephronota.*

two species overlap in the northwest, north, west, southwest, south, and in some parts of central Iran.

(Fig. 2). Outside of the zone of overlap the two species are almost identical. They are identical in pattern, size and shape of the bill, and in general coloration. In relative body size, as shown by the length of the wing, *Sitta tephronota* is slightly larger.

Limiting ourselves for the present to measurements: in the case of the wing, outside of the zone of overlap *Sitta neumayer* measures from 77.5 to 85 mm with an average of 81.7 for 10 specimens of both sexes; *Sitta tephronota* measure 83 to 90 mm with an average of 85.9 for 22 specimens. This, in round numbers, is an average difference of 4 mm. Inside of the zone of overlap, in the case of my longest series, those of the Zagros, *Sitta neumayer* becomes smaller and *Sitta tephronota* larger. The wing measurement in 45 specimens of *Sitta neumayer* is now 73 to 81 mm with an average of 77.2, and in 34 specimens of *Sitta tephronota* 87 to 100.5 mm with an average of 94.0. The average difference between the two species is 17 mm in the zone of overlap instead of 4 mm outside of the zone of overlap.

(Fig. 3). The differences in the bill length are even more striking. Outside of the zone of overlap the bill length in *Sitta neumayer* ranges from about

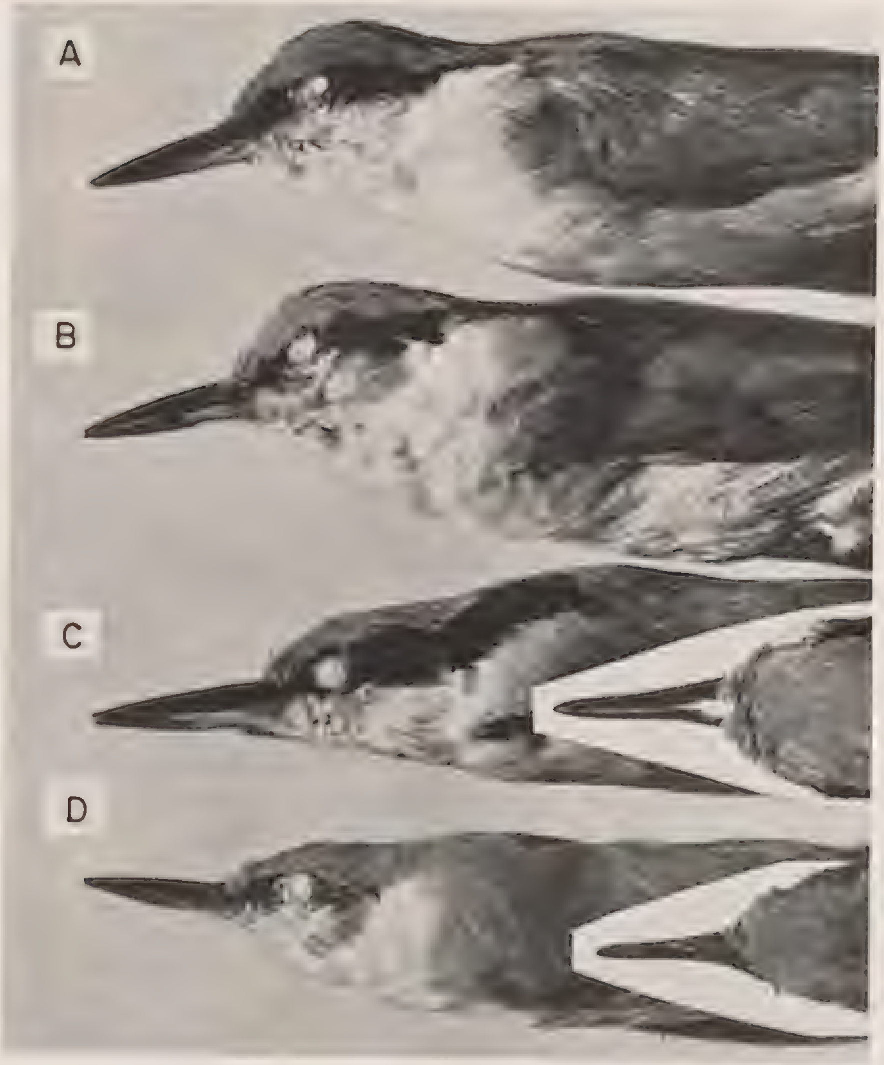


Fig. 2. Size and shape of the bill and facial stripe in *Sitta neumayer* and *S. tephronota:* A, *S. neumayer*, Dalmatia; B, *S. tephronota*, Ferghana; C, *S. tephronota* and D, *S. neumayer* both from Durud, Luristan.

23 to 28 mm with a mean of about 26 mm in the most western populations; in *Sitta tephronota* the range is about the same, the mean being slightly lower, about 25.5 in the most eastern populations. But in the zone of overlap the bill measurements pull very far apart. In the case of the Zagros populations (D and E) the bill measurement in *Sitta neumayer* ranges

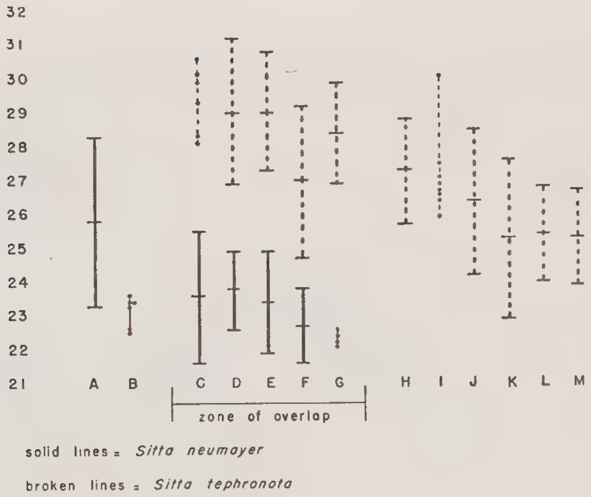


Fig. 3. Graphic illustration of the bill length (measured from skull) in *Sitta neumayer* and *S. tephronota*. Horizontal markings represent the mean and two standard deviations above and below; where sample is insufficient, individual specimens are represented by dots.

Populations west of the zone of overlap (*S. neumayer*): A, Dalmatia and Greece; B, Asia Minor; in the zone of overlap: C, Azerbaijan and northern Iran; D, Kermanshah; E, Luristan and Bakhtiari; F, Fars; G, Kirman. East of the zone of overlap (*S. tephronota*): H, Persian Baluchistan; I, southern Afghanistan (mostly Kandahar); J, Khorasan; K, northcentral Afghanistan; northeastern Afghanistan; M, Ferghana and western Tian Shan.

from 22 to 25 mm with a mean of about 23.5, in the case of *Sitta tephronota* the range is from about 27 to 31 mm with a mean of about 29 mm, a striking difference amounting to almost 20 per cent. In the graph, the horizontal markings represent the mean and two standard deviations above and below, except where the sample was insufficient and actual individual measurements are represented by dots.

It can be seen that these two nuthatches fulfill two of the conditions postulated by David Lack for overlapping species. I have not been able to find information as to the differences in food or feeding habits but certainly the far heavier and longer bill of *Sitta tephronota* strongly implies adaptation to the taking of different food.

(Fig. 2). It was stated that outside of the zone of overlap the pattern, as shown by the facial stripe, was identical. But in the zone of overlap, in the Zagros populations the facial stripe has become almost obsolete in *Sitta neumayer* while it has become very broad and conspicuous in *Sitta tephronota*. This mark, and probably the difference in body size and size of the bill, have a recognition value serving as isolating mechanisms between the two species.

# Some Phylogenetic Trends in Garrulus glandarius Linnaeus and Dendrocopos major (Linnaeus)

*James M. Harrison*

*Sevenoaks, England*

The occasional appearance of morphological characters in birds resembling those found as a constant, in closely related species or subspecies, would appear to indicate a phenomenon of greater importance and deeper significance than that of individual variation as usually manifested.

It is acknowledged that phylogenetic trends are most often expressed in the juvenile plumages of different species, (Stresemann, 1920), and that these transient characters, which throw light upon evolution within the species, mostly vanish when the individual becomes adult, and when persisting into adult life, indicate forms of earlier evolutionary age than those in which such characters are only transient.

The following instances in *Garrulus glandarius* (L.), and *Dendrocopos major* (L.), have come under my notice, but it must be remembered that many more cases can be recognised in a number of other species illustrating this phenomenon.

The first case, Fig. 1, shows a normal Jay, *Garrulus glandarius glandarius* L., and an aberrant specimen of that species. This specimen is a so-called "hairy" albescent, and shows a generally loose character of plumage, with remarkably attenuated primaries, particularly the first.

While of course the surmise in this case is very speculative, the assumption that in evolution early feathers may have been of this hair-like structure is at least possible, while the only other corvine species with such an attenuated first primary is the Magpie, *Pica pica* L., and it is an equally reasonable assumption to deduce that the genus *Pica* may therefore, on the principle already enunciated, have antedated the genus *Garrulus* in evolutionary age.

The wings of *Pica pica* L., *Garrulus glandarius* L., and the aberrant specimen of *Garrulus glandarius* L., are shown in Fig. 2.

A study of juvenile specimens of *Garrulus glandarius* L., provides yet another instance of what would appear to represent an evolutionary ex-

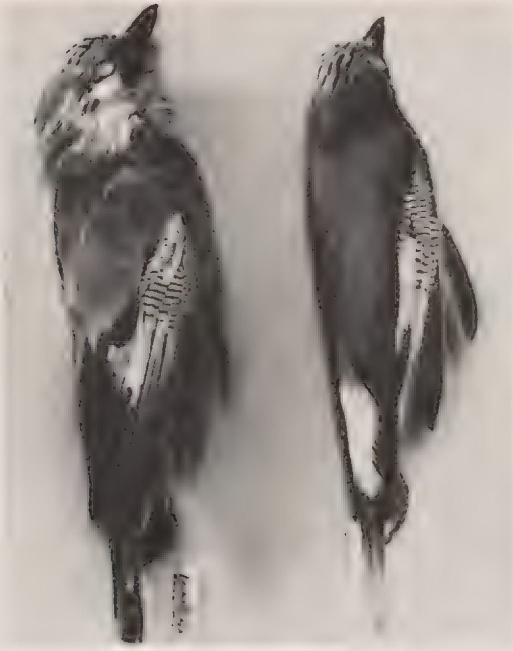


Fig. 1. *Garrulus glandarius glandarius* (L.). Aberrant specimen on left showing loose character of plumage, and attenuation of primaries.

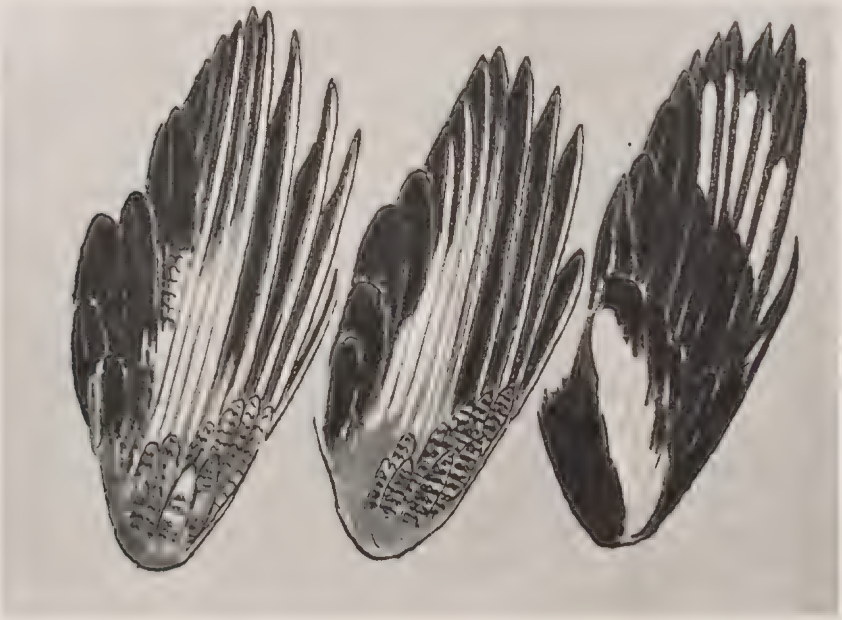


Fig. 2. Diagrammic sketch showing wings of a normal Jay, *Garrulus glandarius* (L.), centre left an aberrant specimen showing attenuation of primaries, especially the first, and right wing of the Magpie, *Pica pica pica* (L.), showing sickle-shaped first primary.

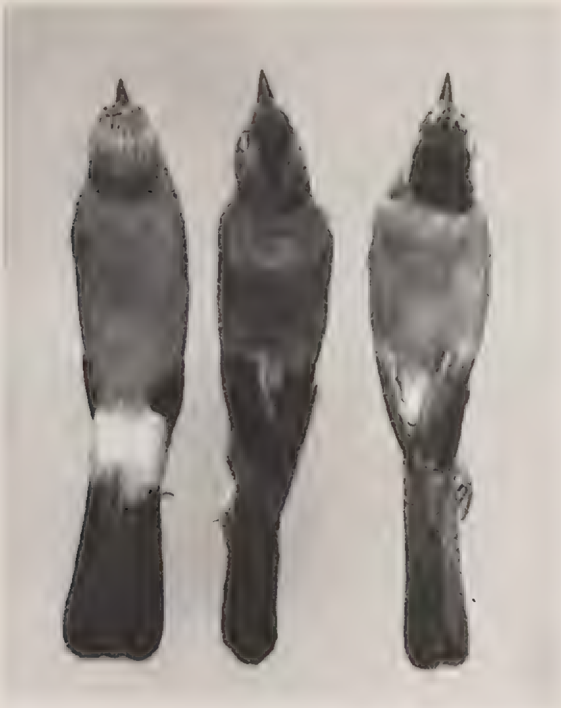


Fig. 3. On left a first winter *G. g. rufitergum* (Hartert), in centre a juvenile of the same race showing in outline a blackish cap. On right an example of *G. g. cervicalis* (Bonaparte), one of the black-capped forms.

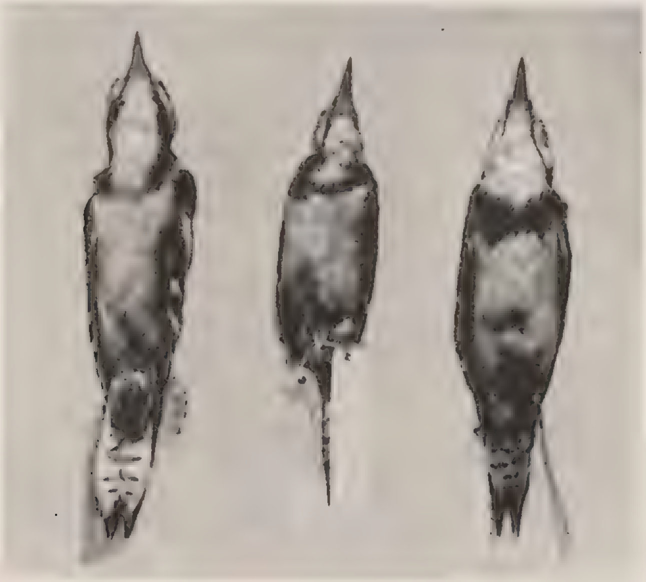


Fig. 4. On the left an example of *Dendrocopos major pinetorum* (Brehm) showing a red crop band, centre and right examples of *D. m. numidus* (Malherbe).

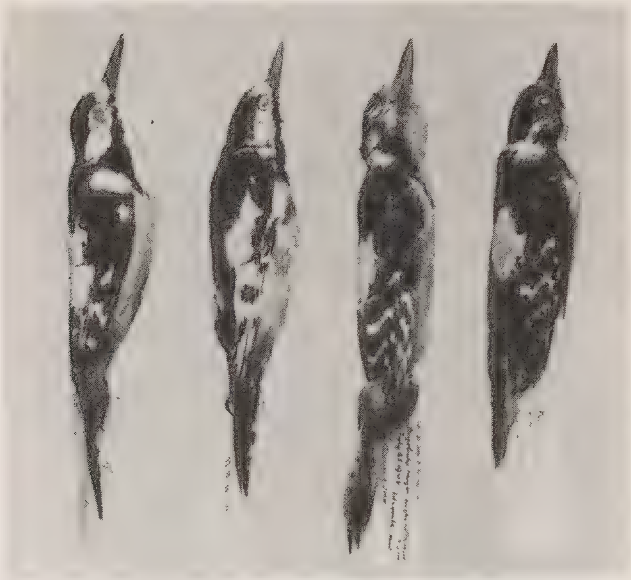


Fig. 5. On right two examples of *D. m. anglicus* (Hartert), showing confluence of white markings on outer vanes of primaries. On left two specimens of *D. leucopterus leucopterus* (Salvadori).

pression. It will be found that a small percentage of immature birds of the European forms of this species, show the outline of the blackish cap, thus indicating a pattern similar to the black cap of certain Asiatic and North African forms, e. g. *Garrulus glandarius cervicalis* Bonaparte.

This condition is shown in Fig. 3, in which, on the left is a first winter example of *Garrulus glandarius rufitergum* Hartert, on the right an example of *Garrulus glandarius cervicalis* Bonaparte and between the two a juvenile *Garrulus glandarius rufitergum* Hartert, showing the outline of a black cap.

I will now deal with the genus *Dendrocopos*, and would remind you of the valuable monograph of Voous (1947), which deals very fully with the history of the distribution of the genus.

An instance of the phenomenon in the species *Dendrocopos major* (Linnaeus) is afforded by the presence of red in the region of the crop, which has been met with in juvenile and first year birds throughout the range of the species.

This character is found as a constant in the North African form *Dendrocopos major numidus* (Malherbe). It is also rather commonly found in *Dendrocopos major mauretanicus* (Brehm) in Morocco, as well as in the populations inhabiting the Iberian peninsula, *Dendrocopos major hispanus* (Schlü-

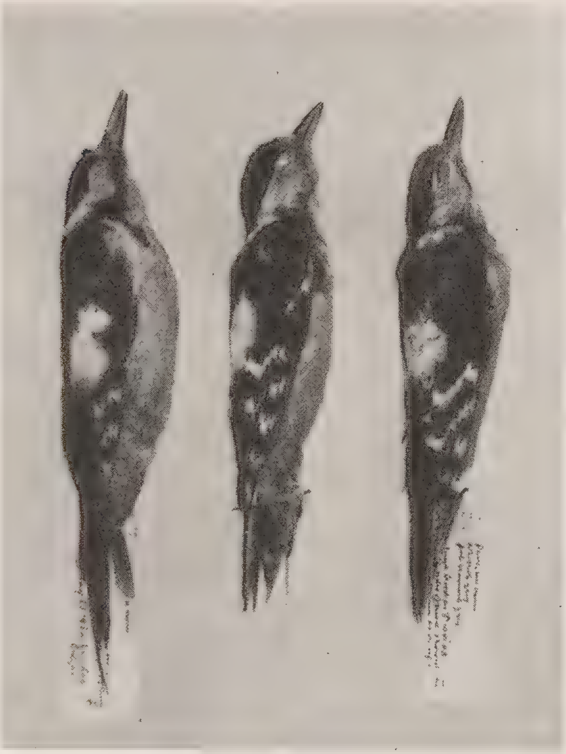


Fig. 6. On right and in centre juvnniles of *D. m. anglicus* (Hartert), belonging to the same brood. Centre specimen showing the face and neck pattern of *D. syriacus* (Hemprich & Ehrenberg). On left an adult female of *D. s. balcanricus* (Gengler & Stresemann).

ter. In *Dendrocopos major numidus* (Malherbe) the red on the crop is found in birds of all ages, i.e. in adults as well as in immatures.

This condition is shown in Fig. 4, in which is to be seen an example of *Dendrocopos major pinetorum* (Brehm), a first year bird, with two specimens of *Dendrocopos major numidus* (Malherbe).

Another character which appears occasionally in the juveniles of *Dendrocopos major* (Linnaeus) is illustrated in Fig. 5. In this case it will be seen that on the outer vanes of some of the primaries the white spots characteristic of the species are replaced by confluent white edges, a character peculiar to the Asiatic species *Dendrocopos leucopterus* (Salvadori). The two specimens showing this aberration are juvenile examples of *Dendrocopos major anglicus* (Hartert), while on the left are two specimens of *Dendrocopos leucopterus leucopterus* (Salvadori). The last example of an aberration resembling a distant species is shown in Fig. 6. In this case the character reproduced in a juvenile of *Dendrocopos major anglicus* (Hartert), the centre specimen of the three, is the unbroken whitish cheek and neck pattern, a character found only in the Asiatic and south-eastern European species *Dendrocopos syriacus* (Hemprich & Ehrenberg), and the races of that species, thus providing a very striking instance of an exact morphological reproduction of a character peculiar to a distant but phylogenetically closely related species.

It is instructive to note that the two juveniles shown in this Figure actually belong to the same brood, and they are shown together with an adult female of the Balkan race *Dendrocopos syriacus balcanicus* (Gengler & Stresemann), which the aberrant specimen so closely resembles.

## Summary

This paper describes certain aberrations in the genera *Garrulus* and *Dendrocopos,* which it is believed throw some light upon the evolutionary trends in those two groups, since in some cases the exact reproduction of characters in distant species or races appear to occur. Whilst of course this subject is highly speculative, the phenomenon described must, it would appear, depend upon some process other than that of fortuitous mutation.

## References

STRESEMANN, E., 1920. Avifauna Macedonica, Munich.

VOOUS, K. H., 1947. On the History of the Distribution of the Genus Dendrocopos (Linnaeus) Amsterdam.

# Ecological Speciation in the Genus Phylloscopus

*W. B. Yapp*

*Department of Zoology, Birmingham*

While geneticists seem to be satisfied that any form of partial isolation of the germ-plasm is adequate for speciation, the general trend of opinion amongst ornithologists at the present time is that geographical isolation of the breeding population is the only type which is of any practial importance. The purpose of the present note is to suggest that in the genus *Phylloscopus,* although difficulties remain whatever view is taken, the present distribution of species and subspecies is best explained as a product of ecological as well as geographical isolation.

The British species *trochilus* and *sibilatrix* have, as is well known, somewhat different habitats, and in some areas where both occur their separation is marked. For instance, both are present in Wyre Forest, in the English West Midlands. This, though much affected by the activities of man, consists in its more natural parts of the oak *Quercus petraea* growing in close canopy, with few associated trees and almost no shrub layer, and a heathy ground flora. Here *sibilatrix* is the only *Phylloscopus.* Where the oaks have been felled, birches, *Betula* spp., regenerate first, and the result is that in places there are thickets of this tree. In these parts *trochilus* alone is found.

This distribution could be explained by supposing that after the two species had evolved in geographical isolation, they met and shared the available ecological niches between them, *sibilatrix* taking the oak forests and *trochilus* the birchwoods, but there is no direct evidence for this view, and there are some facts which suggest that it is unlikely. In the first place, in habitats which are not typical, the two species live side by side. In Wyre Forest they overlap by roadsides, which cannot be characterized botanically as either typical high forest or typical birch scrub, and, even more strikingly, they live side by side in some of the high-level woods of the English Lake District. These are isolated patches of woodland at altitudes of about 300 to 370 m., dominated variously by *Quercus petraea* or *Betula* spp; whether they are relict woods or planted, they are probably very similar to the natural climax vegetation of the hills. The most obvious character that they have in common is that the trees are short (maximum height about 10 m. and most are less than this) so that in spite of the absence of a shrub layer the branches of the trees are near the ground. In these conditions it seems that both *trochilus* and *sibilatrix* can flourish, which suggests that their separation elsewhere is the result of ecological choice, not of competition. If this is so, the ecological distinction looks as if it were a species character. As a further argument against the sharing hypothesis, I would suggest that if two species met in the way proposed it would be likely that one of them would be forced out into a totally new habitat, rather than that a fine division, based chiefly on the dominant species of tree, should be made. In fact there are in Britain, and even more in Europe, a number of habitats which have never been colonized by *Phylloscopus*, although comparable habitats in Asia seem to be not unsuitable for the genus.

These observations on the British species led me to consider the genus more generally, and for the facts on the distribution of other species and subspecies I am indebted to Ticehurst's monograph (1938).

The first fact that strikes one when the distribution is plotted is the high concentration of breeding species in the mountain ranges of India, Tibet, and China. Kashmir has eleven species, Yunnan eight, Kansu eight, and the Mekong-Yangtze region seven, and there are other species in nearby areas. As the genus is on the whole migratory it is difficult to believe that all these species evolved in geographical isolation elsewhere and then met; the simpler explanation is that they evolved in the neighbourhood of their present breeding habitats, and that therefore some other isolating mechanism must have been at work. The information given by Ticehurst, though incomplete, suggests that this might well be ecological.

When one considers the subspecies a number of interesting points emerge. *Borealis borealis* ranges across Northern Europe and Asia from 25° E to 170° E, showing an extreme geographical spread for one subspecies, while *proregulus* has three subspecies, *reguloides* four, and *trochiloides* four, in and around the Himalayas alone. These distributions, though possible, would be unlikely if geographical isolation were the only factor involved.

There are several instances of subspecies which are separated geographically in the breeding season but overlap in their winter ranges. This is true for example of *borealis borealis* and its Japanese relative *borealis xanthodryas*, which both winter in Sumatra, Java and Borneo; four subspecies of *trochiloides*, namely *trochiloides*, *viridanus*, *ludlowi* and *nitidus*, have separate breeding ranges in various parts of Eurasia from the Baltic to Burma, and a somewhat complicated winter overlap in Southern India and Ceylon; and *reguloides assamensis* and *reguloides claudiae*, which in the breeding season appear to be the opposite ends of a cline, have some winter overlap in Yunnan and elsewhere. Such incipient species can hardly be regarded as isolated solely geographically.

Finally, there are a few cases where forms which are considered by Ticehurst to be good subspecies actually breed in the same area. Examples are *trochiloides plumbeitarsus* and *trochiloides viridanus* near the source of the Yenesei, and *fuscatus fuscatus* and *fuscatus weigoldi* in North West Szechwan. In the latter place the two subspecies apparently live at different elevations, *fuscatus* at around 3000 m., and *weigoldi* above this. Ticehurst interprets both these overlaps in terms of the meeting of subspecies evolved elsewhere; their importance seems to me to lie in their proof that recognizable subspecies can live side by side, separated ecologically, but with no barrier between them which an inividual could not pass in a few minutes. If this is granted it seems contrary to the principle of Occam's razor to introduce another isolating factor for which there is no direct evidence. I do not suggest that ecological speciation is proved, but that it is probable, and that in some instances it is the simplest explanation of the facts. It should be worthwhile paying very careful attention to ecological distribution, especially in countries where the vegetation has been little altered by man.

## Reference

Ticehurst, C. B., 1938. A Systematic Review of the Genus Phylloscopus (Willow-warblers or Leaf-warblers). London.

# Evolution of the Hawaiian Honeycreepers (Family Drepanididae)

*Dean Amadon*

*American Museum of National History, New York*

The Hawaiian Islands with their heavy rainfall, great elevation, and position just within the tropics provide an environment rich in plant and animal foods and favorable for songbirds. Yet these islands are so isolated that only a half a dozen kinds of songbirds ever succeeded in colonizing them. Of these few oscine colonists the first was presumably the one that gave rise to the endemic family Drepanididae, which contains some 9 genera and 22 species. Geographical isolation provided by inter-island channels has been necessary for speciation in the Hawaiian honeycreepers, but later many of these species have extended their ranges to other islands and have come into competition with one another. Such competition between related species in an environment containing many empty ecological niches led to the unique adaptive radiation found in the Drepanididae. In this process selection and competition seem to have been the dominant forces and small population genetic effects of no importance (except perhaps in extinction of species at a competitive disadvantage). Pre-adaptation was involved only insofar as the niches which a species may exploit are limited by its anatomy and hereditary make-up. The adaptive radiation of the Drepanididae has been a comparatively rapid process, as is typical of this phase of evolution.

(Extract from a paper in press in Bulletin of the American Museum of Natural History, vol. 95, pp. 151–262, 1950.)

# Distributional and Evolutionary History of the Kingfisher Genus Ceyx in Malaysia

*K. H. Voous*

*Zoological Museum, Amsterdam*

## Introduction

The solution of the problem of the distinguishing characters and the relationship of the Malaysian Forest- or Three-toed Kingfishers of the genus *Ceyx* was strikingly presented by Ripley (1942), who concluded that "*C. erithacus* and *rufidorsus* are closely allied species and might be considered conspecific were it not for the fact that their ranges are overlapping. In the Malay Peninsula, Sumatra and Borneo where this occurs, specimens were examined which show hybrid characters indicating that the earlier confusion in the nomenclature was probably due to this phenomenon" (p. 59). Ripley based his conclusions on the examination of not more than about 70 specimens, all belonging to American museum collections. The personal study of a rather larger material from European collections, comprizing 292 specimens, could happily confirm Ripley's conclusions, but a few additions had to be made, especially regarding the amount of interspecific hybridization in the areas of distributional overlap. Hybridization was found to be considerably commoner than was originally supposed. However, the main aim of this paper is to add some zoogeographical remarks. These remarks are not only given because of the zoogeographical interest of the author, but mainly in order to show that the distributional base of the process of species formation can be traced in this and similar instances, when the systematic arrangement of a group has arrived at a certain stage of perfection. The splendid results in ornithological taxonomy reached during the last ten years must not be the end, but the very starting point of the study of speciation, as it happened in nature.

## Distribution of Hybrids

In table 1 I have followed the distinguishing specific characters summarized by Ripley, which I found to be well-founded. All specimens of *erithacus* lacking either the black frontal mark, the azure-blue patch on the ear-coverts, or showing rufous feathers or spots on the medium or larger upper wing-coverts or on mantle and back have been treated here as potential hybrids. Similarly all specimens of *rufidorsus* showing either a black frontal mark, a blue ear-patch, or black feathers on the upper side have been listed as hybrids.

Table 1

| Locality | Number of specimens | | | Proportions | | |
|---|---|---|---|---|---|---|
| | *Erithacus* | Hybrids | *Rufidorsus* | *Erithacus* | Hybrids | *Rufidorsus* |
| Malaya | 18 | 7 | 12 | 49 % | 19 % | 32 % |
| Sumatra | 12 | 25 | 35 | 17 % | 35 % | 48 % |
| Borneo | 23 | 42 | 8 | 31 % | 58 % | 11 % |
| Labuan | 1 | 10 | 5 | 6 % | 63 % | 31 % |

## Amount of Hybridization

### *Malay Peninsula*

Malayan specimens of *rufidorsus* are less abundant in museum collections than *erithacus*, but they hardly reveal that "it is everywhere a decidedly rarer bird" than *erithacus* (Robinson, 1928, p. 43). *Rufidorsus* does not go farther north than about Bandon Bay, Peninsular Siam; whereas *erithacus* inhabits the lowlands of the whole of continental S.E. Asia.

### *Sumatra*

The number of 12 Sumatran specimens of *erithacus* examined seems to be contradictory to Ripley's view that "the Sumatran records are accidental" (p. 56). These birds, as well as the 25 Sumatran hybrids examined, seem to indicate that *erithacus* is an indigenous Sumatran species, though locally distributed and rather rarer than *rufidorsus*. Hybrids between *erithacus* and *rufidorsus* may represent all intermediate stages between the parent species and are often rather close to specimens of the Bornean race of *erithacus* (*motleyi*).

### *West Sumatran Islands*

In the satellite islands of Sumatra only *rufidorsus* occurs (Simalur, Tana Massa, Tana Bala, Bangkaru, Siberut, Sipora, Pagi Islands), except in Nias, where a race of *erithacus* (*captus*) is indigenous and *rufidorsus* is said to be

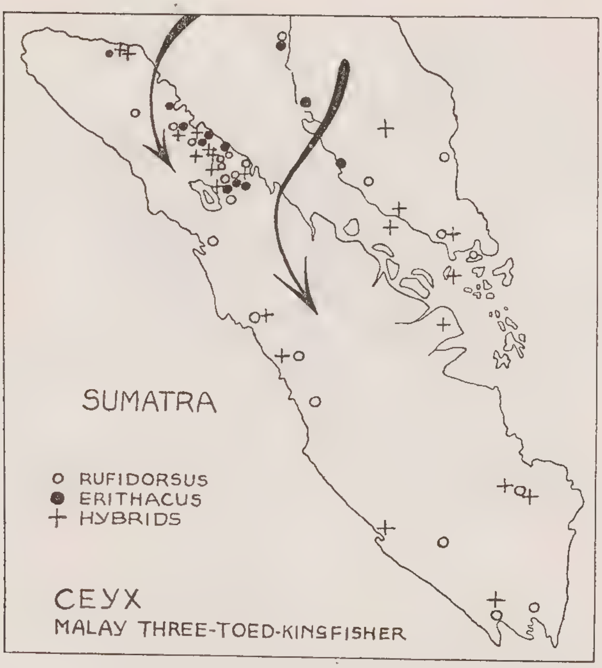


Fig. 1. Distribution of *Ceyx erithacus* and *C. rufidorsus*, as well as their hybrids, according to the localities from which specimens were examined by the author. The arrows indicate the author's suggestion that *C. erithacus* is a rather recent immigrant to Sumatra.

absent (Ripley, 1944). Both species seem to be absent in Enggano Island. Ripley (1942) described *C. rufidorsus jungei* from Simalur Island and the Batu Islands (Tana Massa and Tana Bala), stating that these birds are larger than typical *rufidorsus*. I could confirm this race on the basis of a slightly larger bill. Most of the birds examined from Simalur Island proved to be intermediate between *rufidorsus* and *erithacus*, generally tending towards *rufidorsus*.

### *Billiton Island*

Said to be inhabited by *rufidorsus* only, but 6 out of 11 specimens examined were intermediates.

### *Borneo*

The largest proportion of hybrid specimens seems to occur in Borneo. From this island Ripley also mentions the largest number of his intermediate birds. He described 5 hybrid specimens which "represent almost a com-

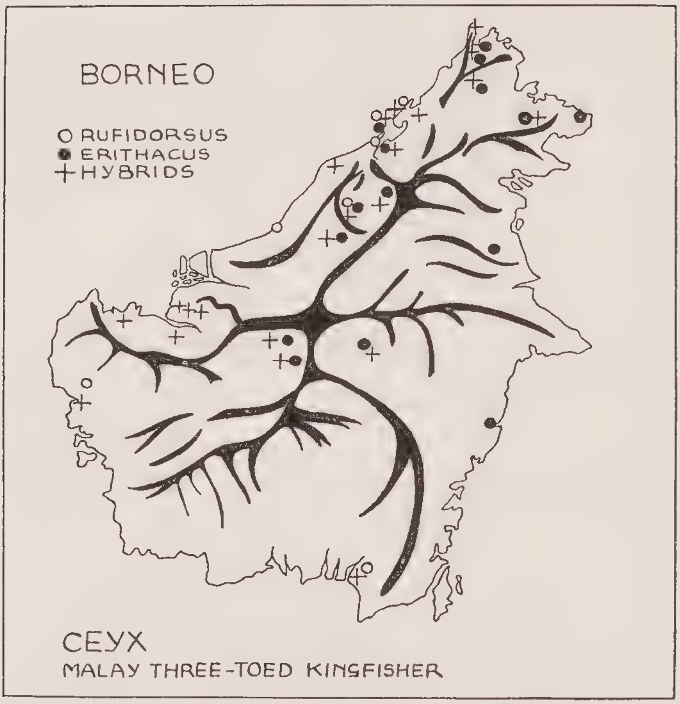


Fig. 2. Distribution of *Ceyx erithacus, C. rufidorsus,* and their hybrids, according to the localities from which specimens were examined by the author. The black lines indicate the main directions of the mountain chains.

plete transition from *erithacus motleyi* to *rufidorsus rufidorsus.*" In the series examined hybrids dominated over the "pure" specimens. Hardly any of the intermediates were alike, exhibiting practically all imaginable character-combinations, showing a most beautiful picture of an interspecific "hybrid swarm." The numerical proportion of *erithacus* and *rufidorsus* in Borneo shows—contrary to the situation in Sumatra—the dominance of *erithacus,* although in Labuan Island *rufidorsus* seems to be the dominant form.

### *Philippine Islands*

Nothing is known of hybridization between *C. erithacus vargasi* and *C. rufidorsus* in Mindoro, the only one of the Philippine Islands where the two species are known to occur alongside each other. However, specimens from Palawan and the Sulu Islands, which are said to be the exclusive home of *rufidorsus,* showed that not all specimens from these islands are morphologically "pure" *rufidorsus.*

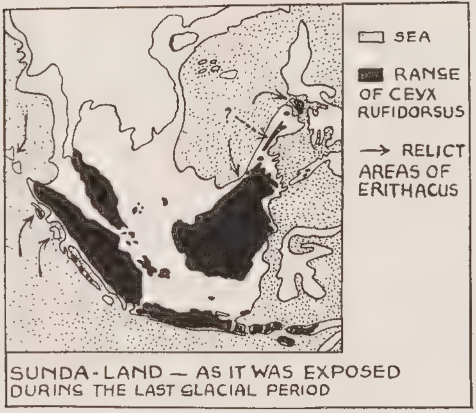

SEA
RANGE OF CEYX RUFIDORSUS
→ RELICT AREAS OF ERITHACUS
?
SUNDA-LAND — AS IT WAS EXPOSED DURING THE LAST GLACIAL PERIOD

Fig. 3. The present distribution of *Ceyx rufidorsus* (black areas), as compared with the land masses which were exposed during the last pleistocene period of low sea level. Relict areas of *C. erithacus* (partly living alongside with *C. rufidorsus*) are indicated by black arrows.

### *Java and Lesser Sunda Island*

Java and the Lesser Sunda Islands are inhabited by *rufidorsus* only, *erithacus* being absent. From 38 Javanese specimens examined 3 birds showed —strange to say—one or more characters of *erithacus*, being about 8 % of the total of specimens examined. Stray characters of *erithacus* in Javanese *rufidorsus* have been found by other authors on previous occasions. From all these specimens the conclusion can hardly be avoided that genes inducing the plumage characters of *erithacus* occur in the populations of *rufidorsus* in Java, though they must be very rare.

### **Systematic Status**

Ripley (1942) was undoubtedly right in stating that *erithacus* and *rufidorsus* do not fit into any of our species concepts. Their pronounced taxonomic difference, in contrast to their large area of distributional overlap with hybridization, places these forms among the most outstanding examples of speciation being a process in which actually living birds participate and not taxonomic characters only. Hence the fact, that the results of active speciation so often do not agree with our artificial and limited schemes of taxonomy. Yet, for practical reasons, the two forms under discussion might best be treated as separate systematic species, as has been done by all previous authors.

## Distribution and Evolution

*Ceyx erithacus* and *Ceyx rufidorsus* occur alongside each other in Malaya, Sumatra and Borneo, but the proportion of their numbers does not seem to be evenly distributed in these areas. As both species apparently occur in the same biotope, living along narrow forest streams and feeding mainly on insects and a few small fishes, the number of specimens present in collections may actually give a rough idea of the numerical proportion of the species in nature. The species forms "hybrid swarms" in regions of distributional overlap, most noteworthily in Borneo.

*C. erithacus* is morphologically more conservative than *rufidorsus.* Most of its range is situated in continental S.E. Asia, from S. China to Ceylon and the Malay Peninsula. Since this area was certainly less disturbed than the Sunda Island area by secondary geographical and climatological influences of the pleistocene glacial periods, this may represent the original range of *erithacus,* or at least part of it. Hence this range may be older than its present occurrence in the Sunda Islands. Its ancestors seem to have emigrated to the Indo-Australian Archipelago from the Asiatic continent. Its original stock is still represented in the Philippines, Moluccas and Papuasia, east towards the Solomon Islands (*lepidus*). The original *C. erithacus* has emigrated to Sunda Land through the Malay Peninsula during one of the pleistocene phases of low sea level. Within the range of Sunda Land relict forms of this species occur at present in the islands of Nias, Simalur (as hybrids), Borneo, and Mindoro. In late pleistocene or holocene times it seems to have re-invaded Sumatra from the continent (see below). The continental origin of *erithacus* in contrast to the Sunda Land origin of *rufidorsus* is also demonstrated by the presence of *erithacus* in the Nicobar and Andaman Islands, where *rufidorsus* is absent. These islands must have been reached by chance flight from the continent.

The complete range of *rufidorsus* covers the whole of the Sunda Land area, including the Lesser Sunda Islands and the Philippines. Contrary to the range of *C. erithacus,* that of *rufidorsus* shows all the characteristics of a late pleistocene range, covering the whole of Sunda Land. At present it is found in almost all insular fragments of this large lowland area: Anamba Islands, North Natuna Islands, Rhio and Lingga Islands, Bangka, Billiton, Kangean, and Bawean Islands; also Balabac and Palawan. Hence the conclusion can hardly be avoided that *rufidorsus* is an autochthonous element in Sunda Land.

As a consequence of the present seemingly unlimited hybridization in the Sunda Land area the suggestion must be made that one of the two species has only relatively recently invaded this area; whereas the other must have been an older inhabitant there. In view of the above-mentioned facts, it is not likely that *rufidorsus* is this new invader. Hence, *erithacus* must have re-invaded the Sunda Land area. This re-invasion must have taken place during the post-pleistocene submergence of the greater part of Sunda Land. Since the Sumatran records of *erithacus* are concentrated in the northeastern part of the island, lying closest to the Malay Peninsula, and the species is known to inhabit coastal mangrove vegetation and small islands, and has been occasionally killed at the lighthouses in the Straits of Malacca (Robinson, 1928), it is almost inevitable to conclude that it is indeed a rather new invader of Sumatra. Radiating from N.E. Sumatra the genes of *erithacus* have rather incipiently spread to other parts of the Sumatran population of *rufidorsus*, becoming less perceptible in the more distant areas. Yet, the—still very rare—*erithacus*-characters found in S. Sumatra and Java are an unmistakable indication of the process of active gene-flow that is going on in the Sumatran and Javanese populations of *rufidorsus*.

*Discussion:*

B. Petersen: Do you think that 65 % of the specimens in one locality can be the hybrids of two species?

K. H. Voous: Although I have proposed to maintain *C. erithacus* and *C. rufidorsus* as distinct species in nomenclature, I have tried to state clearly that I really think they are a border-line case between subspecies and species and that they do not fit into either definitions of these categories.

E. Stresemann in this connection drew attention to the wide-spread hybridization of *Emberiza citrinella* and *E. leucocephala* in Western Siberia.

## References

Ripley, S. D., 1942. A revision of the Kingfishers, *Ceyx erithacus* and *rufidorsus*. Zoologica (New York Zool. Soc.) 27, p. 55–59.

—— 1944. The bird fauna of the West Sumatran Islands. Bull. Mus. Comp. Zool. 94, p. 307–430.

Robinson, H. C., 1928. The birds of the Malay Peninsula. II (London), p. 43.

# Madagascar's Pseudo-sunbird

*Dean Amadon*

*American Museum of National History, New York*

Shelley suggested that the peculiar Madagascar genus *Neodrepanis* may be intermediate between the mesomyodian family Philepittidae and the oscine family Nectariniidae. Examination of an anatomical specimen of *N. coruscans* shows that the genus *Neodrepanis* belongs to the Philepittidae and not to the Nectariniidae, where it has been placed. The tenth primary is long, the aftershaft minute or wanting and the tarsus is taxaspidean. More important, the syrinx has only a pair or two of intrinsic muscles, and these weakly developed. Indeed, the syrinx of *Neodrepanis* is very like that of *Philepitta* as figured by Forbes. The tongue of *Neodrepanis* is highly modified for sucking nectar but does not agree in structure with that of a sunbird (Nectariniidae).

(Summary from paper in press in L'Oiseau et la Revue Française d'Ornithologie.)

# Two races of Bean Goose Anser arvensis in Western Europe

*Robert A. H. Coombes*

*International Wildfowl Research Institute,*
*Zoological Museum, Tring, Herts.*

Rather more than a hundred years ago, the great ornithologist Johann Friedrich Naumann wrote his classic work on the birds of Germany, in it he gave very full descriptions of two forms of Bean Goose, quite apart from the Pink-footed Goose *brachyrhynchus.* One of these geese he called the "Saatgans" *Anser segetum,* and the other the 'Ackergans" *Anser arvensis,* and he stated that both were common winter visitors to Germany. It is clear from his writings that he had considerable field experience of geese, so his views should have carried great weight. However, the leading ornithologists of Europe who succeeded him did not accept his findings, and argued that all the differing characters that he pointed out were simply individual variations within one form of goose. Only the Russian authors, particularly Alpheraky, Buturlin, Stegmann and Tugarinov have given evidence that there are two forms of Bean Goose in European Russia, one breeding in the tundra and the other in the forest zone.

Hartert wrote as follows:—"In spite of all the arguments brought forward in Alpheraky's fine work "Geese of Europe and Asia" *A. fabalis* and *arvensis* are not different species; none of the differences mentioned holds good, both forms are linked by transitional forms and interbreed one with the other, at least on Kolgujev, in N. Scandinavia, and on Nova Zemlya; behaviour and breeding are the same. Most of the later ornithologists agree with my view: Arrigoni, Lönnberg, Miss Jackson, Ogilvie-Grant, Reichenow, Rothschild, Salvadori, Saunders, Seebohm, Sharpe." After Hartert came the works of Schiøler, Heinroth and Witherby, and they also took the same view.

Today I will give you some evidence, which, had it been known to the authors I have just mentioned, would, I think, have caused them to reverse their decisions. In cases where it is possible to prove that all the individuals of a species breeding over a large area have morphological characters differing from the individuals of the same species breeding in another large area, it is universal practice to recognize those two populations as geographical races. But when the breeding grounds are inaccessible to us, as in the present case, I suggest that similar work can sometimes be done in the winter ranges. This applies especially to geese, in which it is usual for the individuals forming a local breeding population, to migrate together and winter together in flocks.

I have been looking for Bean Geese in several countries in each of the last seven winters, and I have found that in one country in Western Europe all the Bean Geese conform to the type which the Russians call the Forest Bean Goose, while in a large area in another country all the Bean Geese conform to the type which the Russians call the Tundra Bean Goose. The number of specimens I have collected in each country is sufficiently large to preclude the possibility of chance. In Great Britain there is in some winters a flock of about 400 Bean Geese in the main concentration area. I sampled this flock in three consecutive winters, collecting 20 specimens, and all of them have the characteristics of the Forest Bean Goose, that is to say the common Bean Goose of Europe, the *arvensis* or *fabalis* type. Furthermore, all the British specimens of Bean Goose that I have examined in the museums in Great Britain belong to the same form. In the museums of Holland and Belgium, however, there are skins of both forms and in north Holland I obtained a few specimens of both forms. But when I reached the provinces of South Holland and Zeeland I began to find large flocks of geese composed entirely of the Tundra Bean Goose, the *segetum* of Naumann and Alpheraky, to which Buturlin in 1933 gave the name *rossicus*. After visiting this area in each of the last four winters, and collecting more than 30 specimens, it is clear to me that the delta of the Rhine and Schelde is the regular winter quarters of large flocks of Bean Geese, and that most if not all of them belong to the tundra form *rossicus*. Last winter the flocks of these geese in the Rhine delta concentrated in a way they have not done in previous years, so that for several days I had the experience of seeing c. 2,000 Tundra Bean Geese assembled together, and observed them under most favourable conditions. In four days I shot 20 of them and a Dutch jäger who was with me shot 5, all these 25 specimens have the morphological characters which the Russian authors associate with the tundra group of Bean Geese.

In addition to these morphological characters I found that the Tundra Bean Geese in the Rhine delta differ from the Forest Bean Geese in Great Britain by occupying a different type of habitat, also they have some different habits and a different voice. I was struck with the fact that the voice of the Tundra Bean Goose is almost exactly like the voice of the Pink-footed Goose *brachyrhynchus*, a fact which goes to support the view of Dr. Johansen and some Russian authors that the Pink-footed Goose is a member of the tundra-Bean Goose group, and that *rossicus* is closely related to it.

Some authors have stated that in their morphological characters the European Bean Geese intergrade completely, and that there are many intermediate specimens that cannot be identified as belonging to one form or the other. I should expect that a few such specimens exist, but I have yet to see more than one or two. Nearly all the Bean Geese that I have examined, and that is more than 150 specimens, can be identified with certainty as to whether they belong to the tundra-group of races or to the forest-group of races. It is only when one tries to differentiate still further within each of those two groups, that the difficulties are great.

However, in Western Europe there is only one representative of each group that could cause any confusion, though it is true that the amount of confusion that those two have caused is rather remarkable. I think that has been largely due to two factors. One is the apparently rather local distribution of the Tundra Bean Goose. So far I have only found it wintering in south Holland and north Belgium, but it must undoubtedly also touch the countries bordering the Baltic on migration to and from north Russia. In the museums in London, Leiden and Brussels there are a number of skins referable to the Tundra Bean Goose, *rossicus*, collected in the delta of the Rhine and Schelde, which show that this has been the predominant form of Bean Goose wintering in that region, since at least the latter part of last century. And it is evident that in Naumann's time flocks of these geese wintered in Anhalt. The only evidence we have to link up with a breeding ground is the head of a Bean Goose brought from the Petchora River by Henry Seebohm in 1875. It exactly matches my series from Holland, and the Petchora tundra is named by Buturlin as one of the breeding-grounds of the Tundra Bean Goose *rossicus*.

The other factor that has perpetuated confusion is that authors have persisted, in spite of Alpheraky's warnings, in trying to differentiate specimens by the quantity or distribution of the yellow colouring on the bill. Pay no attention whatever to the colour on the bill, it will only confuse and mislead, there are plenty of good characters that distinguish the two forms by their measurements. There is not time now to go into the question of the measurements, they must form the subject of another paper, but I will briefly outline the differences between the two forms. The Forest Bean Goose *Anser arvensis arvensis* Brehm is a large goose with long bill, having the nail round and the lower mandible rather straight and not deep. The Tundra Bean Goose *Anser arvensis rossicus* Buturlin is a smaller goose with shorter bill, having the nail long and tapering and the lower mandible more curved and deep, and also fewer teeth.

These differences were described by Naumann long ago and are now confirmed by field work and adequate material.

## References

ALPHERAKY, S., 1905. The Geese of Europe and Asia. (London.)
BUTURLIN, S. A., 1934. Übersicht der Saatgansrassen. Aquila, 1931–34.
COOMBES, R. A. H., 1947. On the Original Description of the Bean Goose. Ibis 89: 272–275.
—— 1947. On the Races of the Bean Goose in the Netherlands. Limosa 20: 229–230.
—— 1948. A note on the status of *Anser arvensis rossicus* Buturlin in the Netherlands. Limosa 21: 101.
HARTERT, E., 1921. Die Vögel der Paläarktischen Fauna. 1903–1938.
JOHANSEN, H., 1945. Om Racer af Sædgaas. Dansk Orn. For. Tidskr. 39: 106–127.
NAUMANN, J. F., 1842. Vögel Deutschlands. Band XI. Leipzig.
TUGARINOV, A., 1932. Tableaux analytiques de la Faune de l'U. R. S. S. Ac. Sc. Leningrad.

# The Populations of the Wedge-Tailed Shearwater (Puffinus pacificus)

*Robert Cushman Murphy*

*American Museum of Natural History, New York*

*Puffinus pacificus,* a petrel of the tropical and subtropical Pacific and Indian Oceans, occupies breeding stations that extend from the Seychelles and Mascarene Islands across 193 degrees of longitude to the Revilla Gigedo Islands, off the coast of Mexico. Most nesting localities are intertropical, but in the Bonin and New Zealand areas of the western Pacific they protrude, respectively, north of the Tropic of Cancer and south of the Tropic of Capricorn (Fig. 1).

Representatives of this species from different localities differ in size, in plumage phase, and in the color of unfeathered integuments. In the Indian Ocean and the part of the Pacific that lies south of the equator, the populations comprise almost exclusively birds of wholly dark plumage. In the northern hemisphere, white-breasted examples become common, the ratio between the two types of plumage being variable. In the Bonin-Formosa district, white-breasted birds approach 100 per cent of the resident populations. A third phase, with a gray or "masked white" ventral surface, also turns up occasionally in the populations.

As taxonomic characters, the three genetic plumage phases are without significance. They represent fluctuating stages of balanced polymorphism and they probably vary temporally as well as spatially.

Twelve specific and subspecific names have been applied to alleged geographic forms of *Puffinus pacificus.* The present study, based upon about 400 specimens of 30 distinct populations, reduces these names to two. Size criteria are tested by the "75 per cent rule," as defined by Amadon (1949, Condor, 51: 250), the terms of which are as follows, in relation to discrete samples of specimens: if the smaller of two means plus 1.88 of its standard deviation does not exceed the larger mean minus 1.88 of its standard deviation, then 97 per cent of one of the populations will be separable from 97 per cent of the other. This corresponds to 75 per cent of one separable

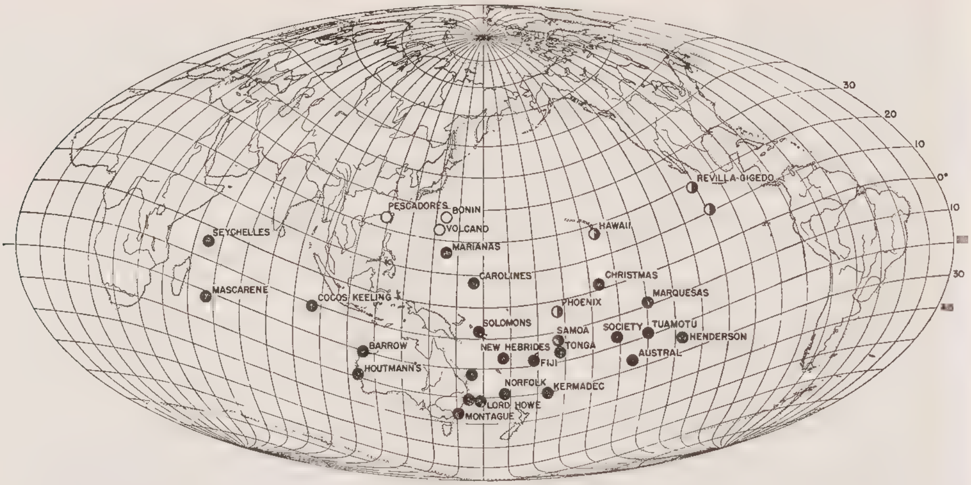


Fig. 1. Breeding range of *Puffinus pacificus.* White circles indicate populations of white-breasted birds, black circles those of all-dark birds. At stations denoted by half black circles birds of both plumage phases are in residence, freely interbreeding. Clipperton Island, south of Revilla Gigedo, is not known to be a nesting station, although examples of the species have been collected on the island.

from 99.9 + per cent of the other. The statistical techniques were applied by the author's assistant, Miss Susan Irving. The results are simplified and reinforced by the fact that *Puffinus pacificus,* unlike many related petrels, does not exhibit sexual dimorphism; i.e. the two sexes are similar in the range and averages of all dimensions.

Many of the numerous breeding populations prove distinct, each from others, as might be expected of oceanic birds segregated as to areas of reproduction. A biological entity such as a freely interbreeding population is not, however, necessarily a taxonomic entity. The variation in size from population to population can in some instances be demonstrated as a cline (Fig. 2).

In the systematic realm, as limited by application of the 75 per cent rule, only two geographic races are recognizable, namely the following:

1. *Puffinus pacificus pacificus*

*Procellaria pacifica* Gmelin, 1789, Syst. Nat., *1,* pt. 2: 560 ("Pacific Ocean." Type locality restricted to Kermadec Islands, Mathews, 1912, Birds Austr., *2:* 80).

Synonyms: *Puffinus chlororhynchus iredalei* Mathews, *Puffinus pacificus whitneyi* Lowe.

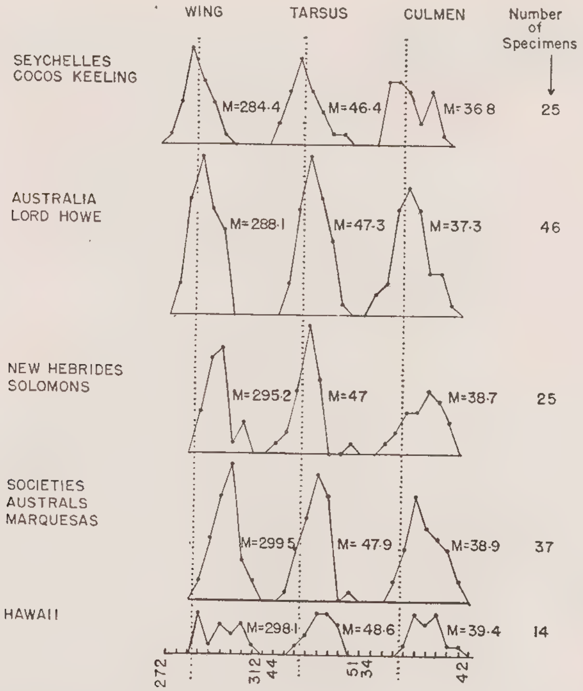


Fig. 2. A cline of increasing size from west to east in ten populations of *Puffinus pacificus chlororhynchus*, as expressed by frequency distribution graphs. The vertical dotted lines represent the means of wing, tarsus, and culmen in the Indian Ocean populations. There is a gradual increase in average dimensions of the birds from the Seychelles to the central Pacific.

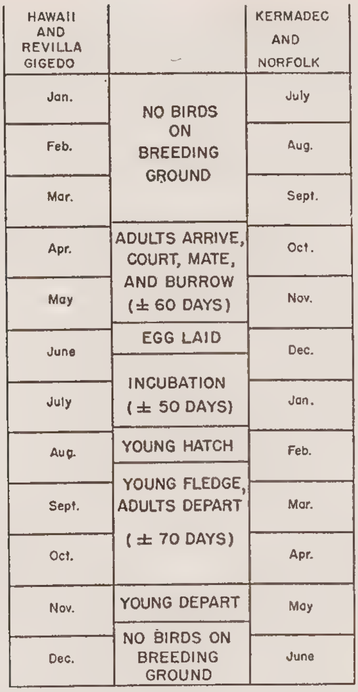
Range: Kermadec and Norfolk Islands, and Kandavu Island of the Fiji group.

2. *Puffinus pacificus chlororhynchus*

*Puffinus chlororhynchus* Lesson, 1831, Traité d'Orn., livr. 8: 613 (Type from Shark's Bay, West Australia).

Synonyms: *Puffinus sphenurus* Gould, *Nectris gama* Bonaparte, *Puffinus cuneatus* Salvin, *Puffinus knudseni* Stejneger, *Puffinus pacificus hamiltoni, P. p. laysani, P. p. alkeni, P. p. royanus,* all of Mathews.

Range: All the known range of the species except the Kermadec, Norfolk, and Kandavu Islands. Specimens have been examined and measured from the following islands or archipelagoes: Seychelles, Mascarene, Cocos Keeling, Australia, Lord Howe, Solomon, New Hebrides, Mariana, Caroline, Bonin, Volcano, Formosa, Tonga, Samoa, Canton, Phoenix, Society, Tua-



| HAWAII AND REVILLA GIGEDO | | KERMADEC AND NORFOLK |
|---|---|---|
| Jan. | NO BIRDS ON BREEDING GROUND | July |
| Feb. | | Aug. |
| Mar. | | Sept. |
| Apr. | ADULTS ARRIVE, COURT, MATE, AND BURROW (± 60 DAYS) | Oct. |
| May | | Nov. |
| June | EGG LAID<br>INCUBATION (± 50 DAYS) | Dec. |
| July | | Jan. |
| Aug. | YOUNG HATCH | Feb. |
| Sept. | YOUNG FLEDGE, ADULTS DEPART (± 70 DAYS) | Mar. |
| Oct. | | Apr. |
| Nov. | YOUNG DEPART | May |
| Dec. | NO BIRDS ON BREEDING GROUND | June |

Fig. 3. Scheme to illustrate the approximate life cycle of two relatively high-latitude populations of *Puffinus pacificus* on either side of the equator.

motu, Henderson, Austral, Marquesas, Christmas Island (Pacific), Hawaii, Revilla Gigedo.

Average measurements of the two subspecies are as follows, the fractions of millimeters being eliminated.

| Adult, both sexes | Wing | Tail | Culmen | Tarsus | Middle toe and claw |
|---|---|---|---|---|---|
| *P. p. pacificus*, 85 .................. | 308 | 137 | 41 | 50 | 60 |
| *P. p. chlororhyncus*, 208.............. | 292 | 133 | 38 | 47 | 57 |

Insufficient details are known regarding the life-history sequences of *Puffinus pacificus* in intertropical localities, but it is evident that the southern-hemisphere cycle prevails at breeding stations well north of the equator. In higher latitudes the stages show a close seasonal correlation and the expected calendar reversal between the northern and southern hemispheres. Figure 3 is an attempt to compare, month by month, the respective régimes of colonies in latitudes 19°–20° North and latitudes 29°–30° South.

(The full text of this abstract will be pulished in 'American Museum Novitates').

# Remarques sur les Cormorans de la région australe américaine

*Christian Jouanin*

*Muséum National d'Histoire Naturelle, Paris*

Ayant eu l'occasion de ranger sous la direction du Professeur Berlioz, la collection d'oiseaux de mer du Muséum de Paris, nous avons examiné plus spécialement les cormorans du groupe *Leucocarbo* Bonaparte que possède ce Musée. Ce matériel permet d'apporter quelques précisions sur les cormorans à «yeux bleus» de l'Amérique du Sud et de l'Antarctique auxquels R. C. Murphy a consacré un chapitre de son ouvrage magistral «Oceanic Birds of South America». Les remarques qui font l'objet de cette communication sont destinées à compléter en quelque sorte certains points de cette excellente étude.

Le Muséum de Paris doit en effet à deux expéditions françaises la possession d'assez nombreux spécimens de ce secteur austral:

— d'une part la Mission Scientifique du Cap Horn (1882–1883), sur «la Romanche», commandée par le Capitaine de Frégate L. F. Martial, qui, parvenue à l'Ile Hoste dans les parages du Cap Horn, se scinda en deux groupes, l'un demeurant dans cette île, à la Baie Orange, du mois de septembre 1882 au mois de septembre 1883, l'autre explorant à bord de «la Romanche», l'archipel du Cap Horn, le Détroit de Magellan et poussant jusqu'aux Iles Falkland.

— d'autre part la deuxième Expédition Antarctique Française (1908–1910)[1] sur le «Pourquoi-Pas?», commandé par le Docteur J. Charcot, qui visita le Détroit de Magellan et les parages du continent antarctique depuis les Iles Shetland du Sud jusqu'au 120° W. G. environ.

Ces deux expéditions ont fait l'objet de publications importantes. L'étude des collections ornithologiques rapportées par la première fut confiée à Oustalet; quant aux récoltes ornithologiques de la seconde, elles ont été l'objet d'un travail de L. Gain qui avait d'ailleurs accompagné ce voyage à titre de naturaliste et avait accumulé une somme considérable de précieuses observations.

---

[1] Nous ne citons pas ici la première expédition antarctique du Dr. Charcot, car la majorité des spécimens d'oiseaux qu'elle rapporta, entre autres la totalité des cormorans, a du être réformée par la suite à cause de leur très mauvais état de conservation.

A l'époque où Oustalet publia le compte-rendu ornithologique de la Mission du Cap Horn, il régnait encore beaucoup de confusion au sujet des cormorans caronculés à «yeux bleux» de l'hémisphère austral et la littérature était fort peu explicite sur les différents types décrits. Voilà sans doute pourquoi Oustalet n'a pas apporté sur les cormorans de ce groupe rapportés par la Mission des vues aussi claires et précises que celles qu'il exposa à propos des *Tachyeres* par exemple, dont il avait fort bien élucidé le problème taxinomique. Il disposa pourtant d'un matériel abondant (beaucoup plus abondant que celui qu'on peut encore consulter maintenant au Muséum de Paris, puisqu'une part importante des récoltes a été donnée depuis, nous l'avons vérifié dans les registres, à différents musées, tant étrangers que français, entre autres au Musée de Cambridge (U. S. A.) et à la Smithsonian Institution de Washington) et aussi des carnets de voyage des naturalistes de la Mission pour compléter les indications de date et de localité qui font parfois défaut sur les étiquettes des spécimens.

Cependant un coup d'œil même superficiel sur l'ouvrage d'Oustalet fournit une indication malheureusement ambiguë: la planche n° 6, intitulée *Phalacrocorax carunculatus,* représente au premier plan un *Ph. albiventer* (Lesson)[1] indiscutable avec la région auriculaire noir-bleu, tandis qu'au second plan se trouve figuré un oiseau référable à la forme *atriceps* King avec les côtés de la tête bien plus largement blancs. Faut-il en conclure que le personnel de la Mission a rencontré aux mêmes endroits exactement ces deux types qu'Oustalet, semble-t-il, assimilait à des variations individuelles?

En fait la Mission du Cap Horn a bien collecté les deux formes, mais la première, *albiventer,* se trouve beaucoup plus abondamment représentée dans le lot qui reste encore au Muséum de Paris. Ce lot comporte en effet sept spécimens de type *albiventer* bien caractérisé pour un seul de type *atriceps.* L'un des *albiventer* a été tué au sud des I. Falkland; cinq autres viennent de la Baie Orange; pour trois de ceux-ci, la date de capture est indiquée: 16 février, 10 mars, 17 mai 1883; la localité du septième n'est pas précisée, mais d'après le numéro d'ordre du voyage il est probable qu'il a été collecté également à la Baie Orange au début de l'été, en 1882. Ces *Ph. albiventer* de la Baie Orange sont respectivement un ♂ adulte, une ♀ adulte, un adulte dont le sexe n'est pas déterminé (ces trois adultes ont une huppe bien développée, et des bandes blanches sur les couvertures alaires), et deux ♂♂ immatures.

---

[1] Rappelons à ce propos, après Oustalet, que le type de *Carbo albiventer* Lesson 1831 des Iles Falkland, signalé par Pucheran dans les collections du Muséum de Paris, a du être réformé, par suite de son très mauvais état, en 1885. Il est donc définitivement perdu et c'est ce qui explique que J. Berlioz ne l'ait pas signalé dans son catalogue des types de Palmipèdes du Muséum de Paris.

L'unique *Ph. atriceps* rapporté par la Mission du Cap Horn que nous ayons retrouvé, est un immature (dont les bandes alaires et la tache dorsale blanches sont déjà discernables) au plumage très usé qui viendrait aussi de la Baie Orange où il aurait été collecté au mois de septembre 1882, d'après le numéro d'ordre du voyage porté sur son étiquette. Il est possible qu'il y ait eu d'autres spécimens de cette forme parmi les oiseaux donnés ultérieurement par le Muséum: la figuration signalée plus haut d'un adulte tendrait à le prouver.

Le Muséum de Paris possède également quelques *Ph. albiventer* provenant de localités diverses de la région fuégienne par l'intermédiaire d'autres voyageurs: un adulte du nord de la Terre de Feu; un immature de Punta Arenas; enfin un ♂ adulte et une ♀ subadulte provenant de la campagne du «Pourqoi-Pas?» en 1910 et tués le 2 février sur la côte du Cap Pillar, dans l'Ile de la Désolation, à l'entrée occidentale du Détroit de Magellan, somme toute au bord de l'Océan Pacifique. Cette dernière localité est, croyons-nous, la plus occidentale des localités de capture de *Ph. albiventer* signalées jusqu'à ce jour.

Chez tous ces spécimens, et bien que la répartition des plages céphaliques noire et blanche soit relativement variable selon les individus, les variations individuelles n'outrepassent jamais certaines limites qui laissent rapporter sans hésitation chacun d'eux à l'une ou à l'autre forme.

Nous donnons ci-après les mesures (en mm) de ces spécimens de *Ph. albiventer* de la Baie Orange et du Cap Pillar qui ne paraissent pas s'écarter notablement des *albiventer* topotypiques des Iles Falkland.

| | | culmen | commissure | tarse | queue | aile |
|---|---|---|---|---|---|---|
| ♂ ad. | Baie Orange | 60 | 87 | — | (très usée) | (très usée) |
| ♂ imm. | Baie Orange | 62,5 | 91 | 61 | 146 | 282 |
| ♂ imm. | Baie Orange | 58 | 89 | 60 | 141 | 280 |
| ad. | Baie Orange | 58 | 89,5 | — | 131 | 268 |
| ♀ ad. | Baie Orange | 61 | 89 | 60 | 136 | 275 |
| ♂ ad. | Cap Pillar | 60 | 90 | 63 | 127 | 291 |
| ♀ subad. | Cap Pillar | 62 | 88 | 57 | 145 | 263 |

Tous ces documents, s'ajoutant à ceux rassemblés par Beck pendant la Brewster-Sanford Expedition, paraissent attester indiscutablement la présence comme nicheur de *Ph. albiventer* dans la région fuégienne. De ce fait, deux interprétations également plausibles restent seules susceptibles d'être envisagées, la conception d'Hellmayr et de Conover, considérant *albiventer* et *atriceps* comme deux sous-espèces, étant plus discutable par suite de cette coexistence:

— ou *Ph. albiventer* et *Ph. atriceps* sont deux formes mutationnelles, en voie d'ailleurs de stabilisation géographique, puisqu'aux Iles Falkland on ne rencontre jamais que la première et sur la côte chilienne, au nord du Détroit de Magellan, que la seconde exclusivement. C'est l'hypothèse que paraissent avoir adoptée différents auteurs comme Oustalet et plus récemment Reynolds;

— ou il s'agit de deux espèces voisines mais toujours distinctes, dont les répartitions géographiques respectives ont une partie commune, où elles offrent peut-être l'exemple d'une segrégation étroitement localisée. Ce point de vue auquel se sont ralliés déjà Peters et Murphy nous semble dans l'état actuel de nos connaissances le plus simple du point de vue de la nomenclature.

Des collections ornithologiques rassemblées par la deuxième Expédition Antarctique Française, il reste au Muséum de Paris, entre autres spécimens dignes d'intérêt, huit peaux de cormorans, collectés à l'île Wiencke le 26 novembre 1909 et à l'île Booth-Wandel le 17 février 1909, et dont Gain a déjà publié des mesures très précises. Parmi ces mesures, celles de la queue, exceptionnellement fortes, s'écartent beaucoup de celles données par Murphy pour *Ph. atriceps* des Iles Shetland du Sud. Aussi cet auteur considérait dubitativement les oiseaux de Gain comme les représentants d'une race distincte.

Nous avons mesuré à notre tour ces cormorans et devons en conclure que Gain ne mesurait certainement pas la queue des oiseaux de la façon la plus courante. Il faut voir là la raison de l'excès systématique de ses mesures.

Voici d'ailleurs les nôtres; la queue est mesurée depuis le point d'insertion des plus longues rectrices, c'est-à-dire les médianes, jusqu'à leur extrémité.

Comparés à des spécimens de la même espèce provenant de Patagonie, les cormorans de l'Antarctique paraissent donc bien avoir la queue un peu plus longue en moyenne, comme l'a signalé Murphy, mais toutefois de façon beaucoup moins frappante que la publication de Gain ne le laissait prévoir. Somme toute ce caractère est assez faible et difficile à apprécier du fait du degré d'usure des plumes chez chaque spécimen et du fait aussi des grandes variations individuelles que le tableau ci-contre met en évi-

| | culmen | commissure | tarse | queue | aile |
|---|---|---|---|---|---|
| ♂ imm. Ile Wiencke | 61 | 94 | 66 | 146 | 307 |
| ♂ imm. Ile Booth-Wandel | 60,5 | 89 | 64 | 167 | 308 |
| ♂ imm. Ile Booth-Wandel | 58 | — | 64 | 148 | 290 |
| ♀ ad. Ile Booth-Wandel | 52 | 79 | 61 | (très usée) | 286 |
| ♀ ad. Ile Wiencke | 52 | 79 | 60 | 131 | 287 |
| ♀ imm. Ile Booth-Wandel | 59 | 82 | 66 | 151 | 300 |
| ♀ imm. Ile Booth-Wandel | 57 | 82 | 63 | 163 | 312 |
| ♀ imm. Ile Booth-Wandel | 55,5 | 89 | 66 | 162 | 312 |

dence. Il est d'ailleurs curieux de constater dans cette série que les deux adultes sont de taille sensiblement plus faible que les six jeunes. Ce curieux état de choses, manifeste même à l'œil nu, peut n'être évidemment que l'effet du hasard, il concorde cependant avec les moyennes relatives de l'ensemble des mesures effectuées par Gain, sur une série plus nombreuse: 13 spécimens, soit 2 ♂♂ et 4 ♀♀ adultes, 4 ♂♂ et 3 ♀♀ juvéniles.

De toute façon cette variabilité individuelle nous suggère d'envisager la longueur de la queue relativement aux dimensions générales de chaque spécimen plutôt qu'en valeur absolue. En effectuant par exemple le rapport $\frac{\text{longueur de la queue}}{\text{dimensions du bec (culmen)}}$ pour nos oiseaux des Iles Wiencke et Booth-Wandel, on constate qu'il varie de 2,4 à 2,9 tandis que pour 2 ♂♂ adultes de Patagonie il est inférieur à 2,2. Cela fait un excès de l'ordre de 10 % en faveur des oiseaux de l'Antarctique. Cet écart est-il suffisant, comparé aux variations individuelles que même la considération du rapport ne parvient pas à masquer, pour justifier la création d'une dénomination subspécifique? Rejoignant encore une fois l'opinion de Murphy, nous pensons qu'il vaut mieux attendre d'un supplément de matériel, permettant une meilleure étude statistique, la réponse à cette question.

*

Outre les cormorans à «yeux bleus» et le *Phalacrocorax magellanicus*, qui appartiennent au même groupe de formes subantarctiques et à affinités néozélandaises, la région fuégienne est encore habitée par un cormoran de type très différent: c'est le *Phalacrocorax brasilianus* (Gmelin) [= *Ph. olivaceus* (Humboldt)], de distribution nettement néotropicale. Les populations de cette espèce habitant la région fuégienne ont été précisément séparées par Murphy de la forme typique sous la dénomination subspécifique *hornensis*. Les spécimens du Muséum de Paris provenant de cette région (Ile Hoste, Terre de Feu, Détroit de Magellan) et de Patagonie argentine (Rio

Santa Cruz)[1] s'accordent avec les mesures données par Murphy pour les types de l'Ile Bertrand et du Canal de Beagle.

Toutefois des spécimens provenant de localités bien plus septentrionales de l'Amérique du Sud ont souvent le bec de taille sensiblement égale. Une ♀ du Lac Titicaca a même le bec encore plus petit (42 mm.), ce qui vient corroborer d'ailleurs une observation de Murphy d'après deux spécimens de la même localité.

Il semble donc que nous soyons en présence d'une espèce dont les populations locales varient fortement et ceci nous amène à douter de la validité des sous-espèces de *Ph. brasilianus* telles qu'elles ont été proposées jusqu'à maintenant.

## Index des ouvrages cités

Berlioz, J., 1929. Catalogue systématique des Types de la Collection d'Oiseaux du Muséum. Bull. Mus. (2), 1, n:o 1.

Gain, 1913. Deuxième Expédition Antarctique Française. Sciences Naturelles: Documents Scientifiques. Oiseaux Antarctiques. Paris.

Hellmayr, 1932. The Birds of Chile. Field Mus. Nat. Hist., Zool. ser., Publ. 308, 19.

Hellmayr & Conover, 1948. Catalogue of Birds of the Americas. Field Mus. Nat. Hist., Zool Ser., Publ. 615, 13, part I, n:o 2.

Murphy, R. C., 1936. Oceanic Birds of South America. New-York.

Oustalet, 1891. Mission Scientifique du Cap Horn. 6: Zoologie. Oiseaux. Paris.

Pucheran, 1850. Etudes sur les types peu connus du Musée de Paris. Rev. Mag. Zool., (2), 2, 1850.

Reynolds, 1935. Notes on the Birds of Cape Horn. Ibis, (13), 5, n:o 1.

Wetmore, A., 1926. Report on a collection of birds made by J. R. Pemberton in Patagonia. Univ. Calif. Publ. Zool., 24, n:o 4.

---

[1] L'un des spécimens a 13 rectrices, alors que le nombre habituel chez l'espèce est 12: ce caractère parait devoir être attribué à une anomalie de la mue. Des exceptions de cet ordre ont été déjà signalées par Wetmore et Murphy.

# Considérations sur la systématique des Turdinés

*Jean Dorst*

*Muséum National d'Histoire Naturelle, Paris*

Dans l'importante famille des Turdidés, (considérée elle-même par certains auteurs modernes à la suite de Hartert comme une sous-famille du vaste ensemble qui, sous le nom de «Muscicapidés» groupe la plupart des insectivores de l'Ancien-monde), il est relativement aisé, malgré quelques formes de passage, de discerner plusieurs groupements secondaires; parmi ceux-ci, les Grives constituent peut-être l'ensemble le mieux tranché (Turdinés): ce sont des oiseaux de taille relativement grande, aux pattes bien développées, en rapport avec leurs habitudes terricoles; leur alimentation est à la fois animale et végétale (baies). La systématique de ce petit groupe peut-être envisagée ainsi.

En tête des Turdinés, nous mettrons à part les *Cichlherminia* Bp, genre unispécifique (*C. L'Herminieri* (Lafr.) ) propre aux Petites Antilles, apparremment très primitifs, aux formes massives, à la queue courte et aux tarses longs; leur plumage a une pattern différente de celle de tous les autres types.

Ayant écarté ce genre aberrant, nous arrivons à un vaste ensemble, groupant quelques genres satellites autour des deux principaux: *Turdus* L. et *Geocichla* Kühl. Ces deux derniers comprennent des oiseaux à queue carrée ou un peu arrondie, jamais très étagée, se distinguant l'un de l'autre par la pattern de la face inférieure de l'aile: celle-ci, chez les *Geocichla* offre une bande blanche caractéristique, qui fait défaut chez les *Turdus.* Ceux-ci ont bien parfois une zone plus ou moins claire sur la face inférieure de l'aile, mais elle reste toujours diffuse. De plus, les *Geocichla* ont les axillaires et les couvertures inférieures de l'aile bicolores, ces plumes étant unicolores chez les *Turdus.* Nous rangeons *T. litsipsirupa* (Smith) dans le genre *Turdus,* car la pattern de la face inférieure de l'aile est bien différente de celle des *Geocichla*: elle présente en effet une vaste tache beige clair, et non blanche, très large et non étroite, contrairement à ce dernier genre; ce n'est au fond qu'une accentuation de l'aspect rencontré chez certains *Turdus*, qui offrent une plage indistincte sur la face inférieure de l'aile (*T. eunomus, T. Naumanni*). Les caractères invoqués pour la séparation générique peuvent paraitre secondaires et un peu conventionnels. Ils sont cependant constants et permettent une séparation nette des deux genres, entre lesquels existent de plus des différences dans la biologie et la distribution géographique.

Par contre, le genre *Hylocichla* Baird, comprenant les Grives tachetées américaines, ne doit pas être maintenu à notre avis; les extrêmes diffèrent certes du type *Turdus* moyen, en particulier par la forme du bec. Mais l'existence de tous les intermédiaires ne permet pas de faire une séparation rigoureuse.

A côté des *Geocichla* et *Turdus* se placent quelques genres plus pauvres en espèces et plus différenciés, *Mimocichla* Scl., remplaçant les *Turdus* dans les Antilles et comprenant des formes à queue allongée et très arrondie, dont les rectrices sont en général terminées de plages blanches. Ce genre, quoique nettement distinct, est apparenté aux *Turdus*, auxquels le relie le genre *Haplocichla* Ridg., ne comportant lui-même qu'une espèce, *H. aurantia* (Gm.), de la Jamaïque et de Haïti, dont les proportions sont assez semblables à celles des *Turdus*, avec la queue néanmoins déjà plus longue et plus étagée; la tache blanche bien marquée de l'aile le fait aisément reconnaître.

Les deux genres précédents se rattachent au type *Turdus*; il en est d'autres qui se rapprochent des *Geocichla*. C'est le cas des *Ixoreus* Bp (= *Hesperocichla* Baird), dont l'unique espèce, *I. naevius* (Gm.), peuple l'Amérique du Nord dans sa partie occidentale, où elle tient la place des *Geocichla* propres à l'Ancien-monde. C'est un type étroitement apparenté aux *Geocichla*, avec lequel il a de nombreux caractères communs (pattern sous-alaire, axillaires bicolores, coloration générale), s'en différenciant principalement par la morphologie du bec (crochet peu marqué, indentation absente; narines en partie emplumées).

Le genre *Ridgwayia* Stj., ne comprenant aussi que *R. pinicola* (Scl.), propre aux montagnes du Mexique, paraît également avoir quelque parenté avec les *Geocichla*, par sa coloration générale, la pattern de la face inférieure de l'aile (mais non des axillaires). Ses tarses sont cependant beaucoup plus courts que ceux des *Geocichla*, en rapport avec ses habitudes arboricoles, et leurs proportions ne sont pas sans rappeler celle des *Sialia*, au voisinage desquels ils sont souvent placés (Sialiinés). Nous croyons que les *Ridgwayia* sont plus proches des *Geocichla* que des *Sialia* bien que constituant apparemment un intermédiaire aux deux groupes.

Enfin nous pensons devoir encore séparer des *Geocichla* le *G. terrestris*

(Kitt.) propre aux îles Bonin, sous le nom générique d'*Aegithocichla* Sharpe (= *Cichlopasser* Bp.); sa pattern est en effet spéciale, le plumage dorsal étant marqué de stries longitudinales foncées, qu'on ne retrouve dans aucun des genres voisins. Notons cependant que la pattern sous-alaire est du type *Geocichla*.

Si nous résumons en un mot la classification des Turdinés, nous pensons devoir les diviser essentiellement en deux groupes (mis à part les *Cichlherminia*, type bien individualisé et primitif), caractérisés morphologiquement par la présence ou l'absence d'une bande blanche sur la face inférieure de l'aile. Ces deux types sont formés essentiellement par les genres *Turdus* et *Geocichla*, autour desquels gravitent quelques genres plus réduits quant au nombre des espèces, et appartenant soit à l'un, soit à l'autre des deux types.

*

A l'intérieur du genre *Turdus*[1], nous pouvons considérer que les formes à plumage tacheté représentent un stade moins avancé que les formes à plumage comprenant des plages nettement distinctes: il s'agit manifestement là de types ayant conservé certains traits de la pattern juvénile, avec évidemment des régressions et modifications. Nous plaçons à la base un ensemble de formes tachetées sur les parties inférieures, comprenant notamment un groupe paléarctique dont *T. viscivorus* L. est le type. C'est également la place que nous assignons à *T. litsipsirupa* (Smith), dont les caractères (pattern sous-alaire) sont suffisamment tranchés pour qu'on le considère comme type d'un sous-genre de *Turdus* (S/G *Psophocichla* Cab.). Une autre lignée est formée par les espèces que l'on peut grouper autour de *T. mustelinus* Gm. et *T. philomelos* Brehm, dont cette dernière est le représentant en Eurasie, avec *T. mupinensis* Laubm., de Chine, mais qui a atteint son plein développement en Amérique du Nord, où elle constitue un type d'oiseau bien différencié.

A ce premier ensemble s'oppose une série de formes que l'on peut grouper autour de *T. chrysolaus* Temm., toutes principalement d'Asie orientale (sauf *T. pilaris* L. d'Europe et de Sibérie occidentale). On y rencontre des espèces encore très peu différenciées au point de vue pattern, telles que *T. eunomus* Temm. et *T. Naumanni* Temm., dont la coloration parait instable et diffuse. La pattern tend cependant à se stabiliser, les caractères pigmentaires se précisent; le plumage comprend souvent des plages d'une coloration rousse bien caractérisée (la coloration rousse est caractéristique de ce groupe, et existe chez toutes les espèces, bien que parfois réduite aux axillaires, comme c'est le cas de *T. unicolor* Tick.): tel *T. chrysolaus* Temm., du Japon, qui peut être pris comme type de cette série.

---

[1] Une étude plus détaillée devant paraitre sur les *Turdus*, nous n'indiquerons que les grandes lignes de la classification de ce genre.

Probablement dérivées du même ensemble sont les formes que l'on peut grouper autour de *T. merula* L. (*T. albocinctus* Royle, *T. torquatus* L., *T. boulboul* Lath., *T. rubrocanus* Gray, *T. Kessleri* Prz.), toutes espèces propres au Sud-est de l'Asie, sauf *T. merula* et *T. torquatus*, qui se sont répandues vers l'ouest, parallèlement à *T. pilaris* pour le groupe *chrysolaus*. Si ce groupe comprend des espèces au plumage encore relativement primitif (*T. merula*), d'autres sont au contraire beaucoup plus évoluées.

On peut rapprocher des ensembles dont nous avons parlé *T. poliocephalus* Lath., espèce polymorphe à vaste distribution dans les régions malaises (sauf Malaisie proprement dite), papoue et océanienne, jusqu'aux Samoa et à la Nlle-Calédonie, mais non d'Australie. Remarquons que c'est la seule espèce malaise et océanienne du genre *Turdus*, se rencontrant soit en montagne, soit dans les régions basses suivant les localités. Elle semble se cantonner dans les hautes altitudes quand existent des *Geocichla* du type *citrina*, qui tiennent leur place à basse altitude dans la région malaise.

En Amérique du Nord, le *T. migratorius* L. paraît être encore un parent probablement assez proche des formes asiatiques, avec lesquelles il offre plus de parentés qu'avec ses congénères de la région néotropicale. C'est une forme à pigmentation très caractéristique, qui effectue des migrations saisonnières.

Tout autres sont les espèces sud-américaines, qui ont évolué séparément en un grand nombre de formes aux différenciations souvent subtiles, remontant au Nord jusqu'au Mexique, et qui sont caractérisées par une pattern assez uniforme, comprenant sur la gorge à fond clair, des stries fines et régulièrement disposées. Les espèces *T. albicollis* Vieil., *nudigenis* Lafr., *fumigatus* Licht., *amaurochalinus* Cab., pour ne citer que les plus représentatives forment le noyau principal de ce vaste ensemble, répandu dans tout le bassin amazonien et les régions andines jusqu'au Mexique. *T. jamaicensis* Gm. les représente à la Jamaïque, qui est ainsi la seule île de la région antillienne où niche un *Turdus*, à l'exception de quelques unes des petites îles les plus proches du continent sud-américain.

Plus remarquables à signaler sont les affinités entre quelques espèces de ce peuplement néotropical — et plus particulièrement *T. rufiventris* Vieil. —, et *T. olivaceus* L., espèce à vaste distribution africaine. Il existe en effet entre ces deux types une similitude complète de proportions, de pattern et de coloration, qui permet un rapprochement faunistique des plus nets entre l'Afrique et l'Amérique tropicale; ce lien, d'autant plus marqué que ce type de *Turdus* n'existe nulle part ailleurs dans le monde, s'intègre dans le cadre des exemples indiquant des parentés faunistiques entre ces deux régions pourtant si distinctes, et qui viennent à l'appui de certaines théories biogéographiques.

En Amérique du Sud, un petit groupe de formes spécialisées en ce qui concerne le bec, qui est fort, large à la base, à arête culminale très peu marquée, a évolué dans les régions andine et patagonienne; ce sont les *T. Falklandi* Q. et G., propres à la région patagonienne, et les espèces voisines des Andes et des montagnes de Colombie (Santa Marta), du Venezuela et des Guyanes (*T. fulviventris* Scl., *T. olivater* Lafr.).

Nous considérerons également comme dérivées de ce groupe les espèces du type *serranus* Tsch. et *fuscater* Lafr. et d'Orb., à aile arrondie, à première rémige très développée, et au plumage intensément coloré en noir ou brunâtre, qui elles aussi habitent la région andine de l'Amérique du Sud.

Enfin un certain nombre de types très particuliers de *Turdus* isolés dans des îles ont conservé des caractères apparemment très primitifs, en particulier au point de vue pattern, avec des proportions différentes, notamment le bec et les tarses plus développés que ceux de leurs homologues. C'est le cas de *T. Bewsheri* Newton, d'Anjouan, de *T. olivaceofuscus* Hartl., de St Thomas et de l'île du Prince, et probablement aussi de *T. maranonicus* Tacz., espèce très particulière du Haut-Marañon, où son isolement lui a permis de conserver un système de coloration unique parmi les Grives sud-américaines.

Nous considérerons comme sous-genre de *Turdus* le *Platycichla flavipes* (Vieil.), d'Amérique du Sud, dont le bec est plus épais, plus large et un peu différent dans sa forme de celui des *Turdus* vrais, et qui présente un cas curieux de dimorphisme mutationnel.

*

Le genre *Geocichla* Kühl a une distribution géographique différente de celle des *Turdus*. C'est un type beaucoup moins ubiquiste, propre à l'Ancien-monde et particulièrement bien représenté dans la région malaise, d'où il s'étend sur l'Asie orientale, la Nlle-Guinée, l'Est de l'Australie et la région éthiopienne, à l'exclusion de la région malgache. Les espèces de ce genre se répartissent, comme les *Turdus*, autour de plusieurs types, dont les deux principaux sont très différents d'aspect l'un de l'autre: un groupe de formes lunulées (ancien genre *Oreocincla* Gould); et un groupe comprenant des formes aux plages de couleurs plus heurtées, d'où résulte un bariolage inhabituel chez les *Turdus*.

Les espèces réunies autrefois sous le nom générique d'*Oreocincla* Gould, sont caractérisées par la présence de lunules noirâtres sur tout le corps (*G. dauma* (Lath.) ), ou seulement sur les parties inférieures (*G. mollissima* (Blyth) ). Dans le cadre de la première de ces espèces se groupe toute une série de formes, les unes à 12, les autres à 14 rectrices (ce caractère pourtant si important dans d'autres groupes paraît avoir perdu toute signification ici et ne délimite au plus que des sous-espèces). Cette espèce étend sa répartition sur l'Asie orientale et le Japon (où elle est d'ailleurs migratrice), l'Asie du S. E., Sumatra et Java, et se retrouve curieusement dans l'Est de l'Australie, en Nlle-Guinée et dans les Salomon, répartition par conséquent discontinue (l'Austro-Malaisie paraissant dépourvue de tels oiseaux), et n'offrant guère d'homologues dans le monde avien.

*G. mollissima* (Blyth) est voisin de *dauma*, mais n'a pas de lunules sur le dos qui est uniforme. C'est une espèce montagnarde de l'Himalaya, de Birmanie et de la Péninsule indochinoise. A son voisinage se placeraient deux espèces encore litigieuses, *G. Dixoni* (G.) et *G. griseiceps* Del., qui peut-être coexistent avec *mollissima* et ne s'en distinguent que par des caractères minimes et assez inconstants.

En Afrique orientale, un petit groupe de formes rappelle davantage les *Turdus* pas sa pattern tachetée sur les parties inférieures: c'est le *G. guttata* (Vig.), d'Afrique orientale et australe, auquel on peut adjoindre le *G. spiloptera* (Blyth), forme propre à Ceylan, qui ne s'en différencie que par des caractères minimes, et bien que plus aberrant, le *G. Princei* (Sharpe), espèce propre à l'Afrique occidentale, où les taches des parties inférieures ont entièrement disparu, mais dont les autres caractères rappellent ceux des deux espèces précédentes.

*G. sibirica* (Pall.), nicheur de Sibérie centrale et du Japon, d'où il émigre dans toute l'Asie méridionale pendant l'hiver, constitue un type très particulier de *Geocichla*, sans proches parents. Le plumage du mâle, très différent de celui de la femelle, ne ressemble à celui d'aucune autre espèce. On a souvent voulu le rapprocher de *G. interpres* et *G. schistacea*, dont il est en réalité bien distinct par la forme du bec si caractéristique de toutes ces espèces malaises. Rappelons que la ♀ a un plumage qui ressemble à celui qu'on trouve chez les *Zoothera* (*Z. marginata*). On peut rapprocher *sibirica* de *G. Wardi* (Jerdon), espèce distincte indienne vivant dans l'Himalaya, bien qu'elle soit assez distincte.

Nous arrivons enfin aux *Geocichla* proprement dits, espèces à pattern parfois assez compliquée, et dont le bec est en général plus court et plus large à la base que celui de tous les types précédents. C'est un groupe essentiellement indo-malais, qui s'étend à l'Est jusqu'aux Moluques et à toutes les Petites îles de la Sonde.

*G. interpres* (Temm.) peut être considéré comme type de ce groupe; sa pattern et ses proportions générales se retrouvent chez toute une série de formes échelonnées depuis la Malaisie jusqu'aux Moluques et aux îles Tenimber, mais qui restent étrangères à la Nlle-Guinée, toutes les espèces de ce groupe paraissant être des représentants géographiques d'un même type, bien qu'évoluées depuis assez longtemps pour être nettement diversifiées. C'est ainsi qu'*interpres* (Temm.) habite la région proprement malaise, les Petites îles de la Sonde et les Philippines; *G. schistacea* Meyer, Timorlaut (?*Machiki* selon Seebohm); *G. erythronota* Scl., Célèbes et l'île Peling; *G. Dohertyi* Hart., Lombok et Sumbawa; *G. Dumasi* Roth., les Moluques; *G. Peroni* (Vieil.), Dammar et Timor. Nous rapprocherons de ces formes les espèces africaines, à coloration d'un roux plus ou moins vif et à taches claires bien marquées sur l'aile. Telles les différentes formes de *G. Gurneyi* (Hartl.), d'Afrique orientale et australe, dont une sous-espèce est propre au Mt Cameroun, nouvel exemple des affinités faunistiques qui existent entre le Mt Cameroun et les montagnes de l'Est africain. A côté de ces formes propres, en général, aux forêts d'altitude, il existe dans la région forestière basse du Sud-Cameroun une espèce voisine, *G. camaronensis* Sharpe; comme leurs homologues malaises, toutes ces Grives terrestres africaines sont donc des oiseaux propres au biotope densément boisé.

Une place à part peut être faite à *G. citrina* (Lath.), espèce typiquement indo-malaise, ne débordant pas sur la région océanienne au delà de la ligne de Wallace. Sa pattern simplifiée et sa coloration tranchée le font aisément reconnaître. C'est une espèce caractéristique des régions de basse et moyenne altitude, où elle parait tenir la place des *Turdus*. Très évoluée, elle représente certainement un type particulièrement différencié.

Plus éloigné de toutes les espèces précédentes, le *G. Everetti* Sharpe, de Bornéo, offre une pattern qui n'est pas sans rappeler celle de certains *Turdus* (gorge striée). La coloration du dessous de l'aile est par contre typiquement celle des *Geocichla*. Le bec est fort, allongé, et ressemble un peu à celui des espèces suivantes.

Un dernier groupe de *Geocichla* comprend 3 espèces assez particulières, habitant les zones montagneuses de l'Himalaya, du Yunnan (*monticola* (Vig.) ); de la Birmanie et des zones montagneuses de la Péninsule indochinoise (*marginata* (Blyth) ); et de Sumatra, Java, Lombok et Mindanao (*Andromedae* (Temm.) ). Ces 3 espèces sont assez bien différenciées pour que l'on puisse conserver pour elles un sous-genre spécial, *Zoothera* Vig., qui se différencie par un bec fort, très allongé et comprimé latéralement; et des vibrisses rictales nombreuses, recouvrant partiellement les narines. La bande blanche de la face inférieure de l'aile est très variablement développée: nette chez *Andromedae*, elle est beaucoup moins marquée chez *marginata*, où elle est fortement teintée de roux-beige, plus large, avec des bords moins bien définis.

Ce groupe paraît assez primitif, notamment au point de vue coloration. La morphologie de son bec en fait un type très spécial, mais qu'on ne peut séparer génériquement, *G.(Z.) Andromedae* (Temm.), pourtant si individualisé par ailleurs, étant en quelque sorte intermédiaire entre ces espèces et le type moyen de *Geocichla*.

*Discussion:*

Delacour: *Ixoreus naevius* est tout à fait semblable de forme, de proportions, de pattern et d'habitudes aux *Geocichla* asiatiques. — It should be called *Geocichla*.

# The Mallophaga as an Aid to the Classification of Birds with Special Reference to the Structure of Feathers

*Theresa Clay*

*British Museum (Natural History), London*

## Introduction

The object of this lecture is to bring to the notice of ornithologists both the use of the general principle that the phylogenetic relationships of the Mallophaga reflect those of their hosts and the limitations of the application of this rule; and further to discuss some of the problems with which the parasitologist is faced—problems which can be solved only by the ornithologist.

## Evolution and present distribution of the Mallophaga

The present distribution and host relationships of the Mallophaga suggest that the evolution of this group must have taken place on certain lines (see Clay, 1949) resulting in related groups of birds being parasitized by related species of Mallophaga. The exceptions to this general rule can be explained by discontinuous distribution, secondary infestations, and parallel and convergent evolution (Hopkins, 1942; Clay, 1949).

## The role of certain environmental factors in the evolution and distribution of the Mallophaga

The environment of the Mallophaga is formed by the external characters of the body of the bird and, hence, the evolution of the Mallophaga has been influenced by certain superficial characters of the hosts irrespective of whether these are of phylogenetic importance. The following are some general reactions, found throughout the Mallophaga, to certain characters of their environment.

1. Size. Harrison (1915: 96) was the first to point out that in a genus of Mallophaga distributed over a number of nearly related birds, the size of the parasite is roughly proportional to the size of the host. This principle

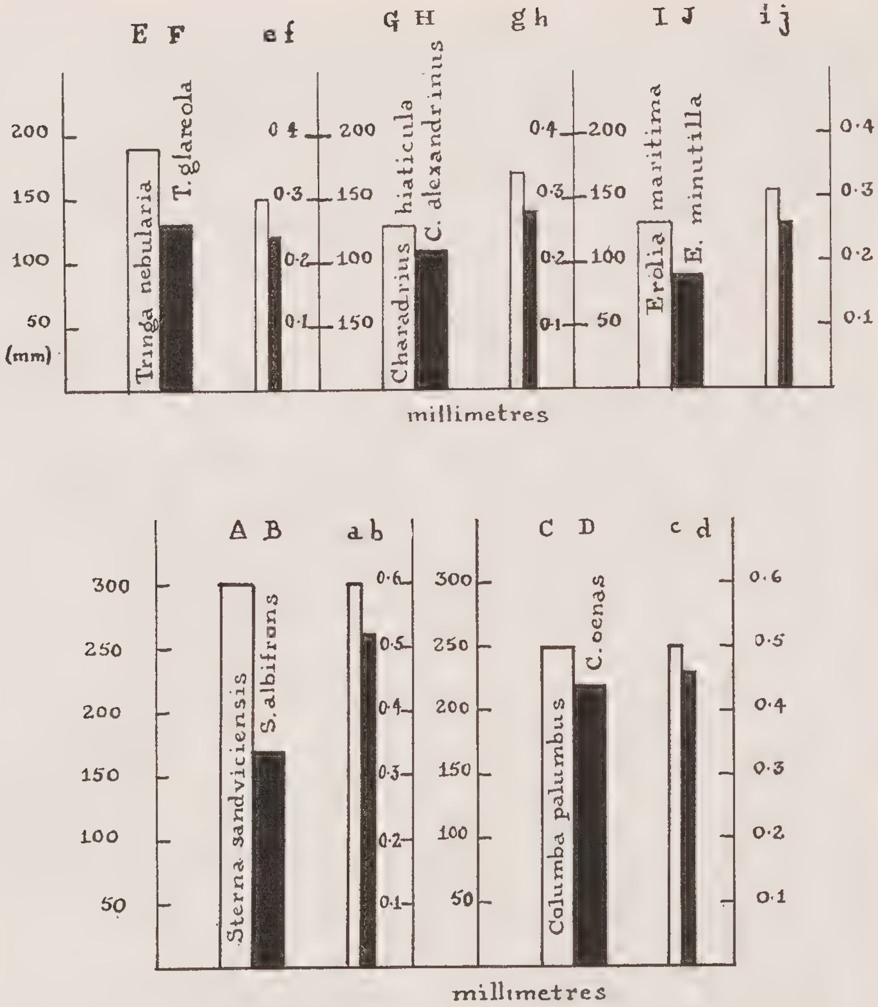


Fig. 1. Examples of the general relation in size between host species and parasite species. (Calculated from the mean of the lengths of wings of hosts and breadth of heads of parasites.) a–j. parasite species: a–b. *Saemundssonia* spp.; c–d. *Campanulotes* spp.; e–h. *Quadraceps* spp.; i–j. *Carduiceps* spp. A–J host species.

has a wide application throughout the Ischnocera and some examples are shown in figure 1. Although in these cases there is little or no overlap in measurements between the two Mallophaga species, in other cases the means of the measurements may be distinct, but there is an overlap in the range of measurements (fig. 2), or the difference in measurements may be

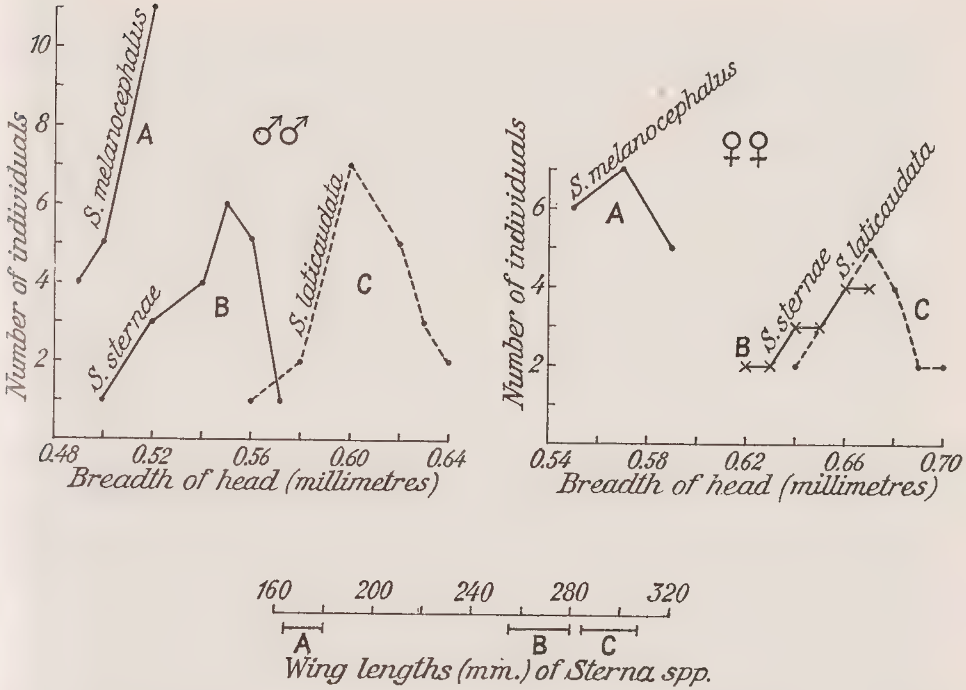


Fig. 2. Differences in size of male and female parasite (*Saemundssonia* ssp.) in relation to size of host. A. *Sterna albifrons*, B. *Sterna hirundo*, C. *Sterna sandvicensis*.

shown in one sex only (fig. 2). Thus, measurements showing this correlation between size of host and parasite need careful analysis. It is not possible, therefore, to do more than make some suggestions of its cause: Size of parts of the feathers: Little seems to be known about the size of parts of the feathers in nearly related birds. Rensch (1924) has shown that the larger races of a species have a greater number of larger cells in the feathers than the smaller races of the same species, which presumably would mean an increase in the size of individual parts of the feather such as the barbules. Size of the barbules, as the latter are eaten by the Mallophaga, might directly affect the size of certain structures used in feeding, the increased or decreased size of which would be reflected in the size of the whole animal. The difficulties in accepting this theory is that the presumed optimum size appears to be different for males and females, and the range of size in some species seems rather large. Temperature of the body of the host: Wetmore (1922) has shown that larger birds in general have lower temperatures; if this is true for related species of birds, the occurrence of the

Table I. The distribution of the "*Clayiella*" group (+) of *Philopterus* on the Momotidae and the Passeriformes. Where no species of *Philopterus* has been seen from a family, this family is omitted from the list.

| | | | | | |
|---|---|---|---|---|---|
| Momotidae. | + | Corvidae. | | Muscicapidae. | |
| Formicariidae. | + | Paradiseidae. | + | Prunellidae. | |
| Cotingidae. | + | Paridae. | | Motacillidae. | |
| Tyrannidae. | + | Timaliidae. | | Bombycillidae. | |
| Pittidae. | + | Pycnonotidae. | + | Laniidae. | |
| Alaudidae. | | Cinclidae. | + | Nectariniidae. | + |
| Hirundinidae. | | Mimidae. | | Dicaeidae. | + |
| Campephagidae. | + | Turdidae. | | Ploceidae. | |
| Dicruridae. | | Sylviidae. | | Icteridae. | |
| Oriolidae. | | Regulidae. | | Fringillidae. | |

larger parasite on the larger host might be explained by Bergmann's law—the larger species being found in the colder climate. Whether there is, in fact, a significant temperature difference between say *Columba palumbus* and *C. oenas* must wait for further work on the subject of birds' temperatures.

2. Colour. It is well established that, in many cases, there is a direct correlation between colour of the plumage of the host and colour of the Mallophaga species (Eichler, 1936; Clay, 1940: 33).

3. Texture of Feathers. There is some evidence that heavy sclerotization and sculpturing of the surface in certain Mallophaga is caused by iridescent feathers (see *Lagopoecus* from *Lophophorus impeyanus*, *Goniocotes* from *L. impeyanus* and *Tragopan satyra*; genera of Mallophaga found on the iridescent members of the Paradiseidae). Feather texture may in some cases be responsible for the development of similar morphological characters of the head in a number of species belonging to the same genus parasitizing not closely related hosts. Table I gives the distribution of the "*Clayiella*" group[1] of *Philopterus*; it is obvious that the families so parasitized do not form a natural taxonomic group, and it seems likely that they have some common feature in the structure of their feathers (some at least show iridescence of the feathers) which has resulted in modifications of their parasites on similar lines.

## Feather structure

Chandler (1916) has shown that the details of the structure of certain parts of the feathers can be used in taxonomy. The down barbules especially show modifications and he states (:387): "it is frequently possible by means of the down alone to identify the group to which a bird belongs." Chandler has also discussed the relationships of the class Aves using this one character of the minute structure of the feathers, admitting of course that no classification can be based on one character, but suggesting that it should be taken into account and may help to bridge the gaps left by other comparative studies. It is of interest that some of Chandler's suggested alterations in the usually accepted classification of the class are supported by evidence from the distribution of the Mallophaga. Are there, however, causes, other than relationship between the hosts, which might be responsible for the Mallophaga reflecting this simularity between the feather structure of their hosts?

---

[1] This group of species differs from the rest of the genus *Philopterus* in certain characters of the head, but as these characters have probably arisen independently in the species found on the different families and are adaptive and not phylogenetic, the group cannot be recognised as a genus.

Relationship between the genera of Mallophaga. It is obvious that unless the relationships between the genera of Mallophaga themselves are correctly evaluated any deductions of host relationships will be invalidated. The most important point to be emphasized is that in the largest superfamily of the Mallophaga (the Ischnocera), containing over a hundred genera, most of the genera are basically similar in both their external and internal morphology, and that there are many groups (say subfamilies) in which the genera are distinguished from each other by very minor characters. Some of these subfamilies, for example the Degeeriellinae, have a wide distribution throughout the class Aves, and further, probably formed the ancestral stocks giving rise to many genera, the affinities of which are now obscure. It is for this reason that only in a few cases does the distribution of the Mallophaga throw any light on the relationships between orders of birds as now recognised. It seems probable that no great divergence took place in the Ischnoceran Malloghaga until after the stocks giving rise to many of the modern avian orders had separated, possibly because until then there was no great divergence in feather structure. In many cases such ancestral avian stocks seem to have been parasitized by only one Ischnoceran genus—it being pure chance which of the few genera on the parent avian stock happened to be on that part of the population which was isolated and ultimately gave rise to the order as now known. This single Mallophagan stock diverged into several genera and filled the different ecological niches on the body of the bird; this has resulted in all such genera on one order being more closely related to each other than to those on any other order. The Mallophaga of the Psittaciformes are probably an example of such a case.

We can now consider what might have happened to such an ancestral Mallophagan stock isolated on a group of hosts and subjected throughout a long era of time to the different environments found on the bodies of the hosts:

a. Cessation of Evolution. The primitive type of Mallophagan head has a complete line of thickening (marginal band) round the anterior margin (the so-called circumfasciate head) and the thickening (ventral band) supporting the pulvinus (a structure of great importance in feeding) is complete. Specialization has taken place by the interruption of these bands of thickening. It would seem that these modifications are advantageous to the parasites on the majority of bird orders as there are only four host groups on which the parasite genera with unmodified heads are dominant. These are the Sphenisciformes, the Tinamiformes, the Galli and the Columbae; the last three groups also have other parasite genera with modified heads. The Procellariiformes have one genus (*Episbates*) in which the head is scarcely modified, but all the other genera on this order, and all other known genera from the rest of the Aves have Ischnoceran genera in which the head is in someway modified even if it is only the median interruption of the ventral band. Chandler has shown that the Tinamiformes, Galli and Columbae (parasitized by Mallophaga with the more primitive heads) all have a similar type of down with a very typical structure. Without discussing whether this fact denotes a relationship between the Tinamiformes, Galli and Columbae, it may prove that the primitive type of head is best suited to this feather structure and thus has a selective value which has prevented the modifications found in genera on other host orders. Further evidence that this may be true is given by the Mallophaga of other bird groups: Chandler (1916: 347) shows that the down of the Rhamphastidae is somewhat similar to that of the former three groups of birds, and it is therefore of interest that the head louse of this family (*Austrophilopterus*) is unusual in having the preantennal region not greatly modified. Chandler also shows that birds belonging to the Coraciidae, Trogoniformes, Momotidae, Meropidae and Upupidae show affinities in the structure of the feathers of the back to both the Cuculiformes and some of the Galliformes, and he also shows (1916: 377) that some of the Falconoidea show a feather structure similar to the Galli, although he does not suggest that this latter case indicates relationship. In all these bird groups, with the exception of the Momotidae and Meropidae, the dominant genera of body lice show the circumfasciate head. Thus, if the structure of the feathers favours the retention of the more primitive type of head, the genera concerned, because of the simularity of the rest of their morphology, will appear to be more closely related to each other than to those in which the head has become specialized, possibly in response to a different feather structure. This may be one of the causes of erroneous deductions of host relationships from those of their parasites.

b. Parallel Evolution. Alternatively to the cessation of evolution due to the simularity of feather structure, evolution of the members of one subfamily (with a wide distribution) may have taken place on parallel lines in response to the same feather structure (see Clay, 1949). Thus, two not closely related groups of birds with simularity in the structure of their feathers (not denoting relationship) might have apparently closely related Mallophaga.

c. Divergent Evolution. Some members of a host group might show divergence in feather structure, of no great phylogenetic importance, which might be responsible for modifications in the morphology of the louse populations. The latter would then appear not to be closely related to the populations on related host groups. Hence, a group of birds with a Mallophagan fauna which does not appear to be related to any other does not necessarily mean that the hosts occupy an isolated position in the class Aves; there are several groups, for example the Caprimulgiformes, Alcedinidae, Coliiformes and Apodi, where the Mallophaga give no clue to the affinities of their hosts.

## Conclusions

The arguments for and against the use of the distribution of the Mallophaga as an aid to the classification of birds can be summed up as follows:

### Arguments in favour

1. That in the great majority of cases the principle that the Mallophaga of related hosts are themselves related is true, and that it is possible to tell from the Mallophaga to what order a bird belongs. Hence, the distribution of the Mallophaga should carry a considerable amount of weight in those cases where the ornithologist is in doubt over the correct systematic position of a bird.

2. In most cases where a bird has an apparently anomalous Mallophagan fauna, there is found to be a difference of opinion over its correct systematic position, and in these cases the evidence from the Mallophaga usually support one of the opinions as to the relationship of the bird in question advanced by the ornithologists.

### Arguments against

1. A great many of the genera of Mallophaga apparently confined to one group of related hosts, actually belong to subfamilies with a wide distribution throughout the class Aves, the differences between them being due,

most probably, partly to feather structure and partly to the time they have been isolated. Hosts with similar feather structure (if this does not denote relationship) might be parasitized by Mallophaga appearing to be related to each other because they had retained the primitive form of head or evolved on parallel lines. Again, hosts which had developed diverse characters in their feather structure might be parasitized by aberrant forms of Mallophaga.

2. Hosts with similar feather structure (if this does not denote relationship) might be parasitized by related Mallophaga because secondary infestation had taken place, this being made possible by the simularity of the environment—feather structure probably being one of the factors limiting the establishment of host specific species on a new host.

3. A genus of Mallophaga may show a discontinuous distribution either because it has become extinct on certain bird groups, or it may have been accidentally eliminated because it happened to be absent on the population which gave rise to a new bird group. These cases of the discontinous distribution of once widely distributed genera will give a false idea of relationships between hosts.

These remarks on the influence of feather structure on the evolution of the Mallophaga must be of a tentative nature as too little is known both about the Mallophaga and the minute feather structure of many birds. It can be said, however, that although some cases of simularity between the Mallophaga species may be traceable to simularity of feather structure a study of Chandler's results will show that there are many exceptions: for example, the simularity of the down of the divers (Gaviiformes *sensu* Wetmore, 1940) and penguins is not reflected by the Mallophagan parasites; nor is the simularity of the down of *Eurypyga* to certain Ardeae. In the majority of cases where the evidence from the Mallophaga support Chandler's emendations to the usually accepted classification of the Aves, there is also supporting evidence from other anatomical features of the bird—presumptive evidence that the Mallophaga are showing phylogenetic relationships not adaptations to a simular feature of the environment.

*Discussion:*

G. Kramer asked if transplantation of Mallophaga from one host to another has been tried. This would be very important in order to prove or disprove the possibility of secondary infestation.

T. Clay: Few experiments of keeping Mallophaga on the feathers of strange hosts have been carried out. Except in the case of related hosts such as chickens and guinea fowls the Mallophaga have died and been unable to breed.

R. Meinertzhagen: The young cuckoo has no contact with its parents and therefore is not infested with cuckoo-Mallophaga during the first few months of its life. But young cuckoos are often infested with Mallophaga from its foster parents and from air-borne infestation by Hippoboscid flies. But in no case have these stragglers been found on adult cuckoos, tending to show that natural straggling and successfull acclimatisation is a rare exception.

W. Yapp: Where there have been successfull experimental transfer of Mallophaga, have there been any changes in form comparable to those which are alleged to have been produced by transfer of *Pediculus* from head to body and vice versa?

T. Clay: Too little is known about this subject to give an adequate answer.

## References

Chandler, A. C., 1916. A study of the structure of feathers, with reference to their taxonomic significance. Univ. Calif. Publ. Zool. 13: 243–446.

Clay, T., 1940. Genera and species of Mallophaga occurring on Gallinaceous hosts. — Part II. Proc. zool. Soc. Lond. 110 (b): 1–120.

—— 1949. Some problems in the evolution of a group of ectoparasites. Evolution, 3: 279-299.

Eichler, W., 1936. Die Biologie der Federlinge. J. Orn. Lpz. 84: 471–505.

Harrison, L., 1915. Mallophaga from Apteryx, and their significance. Parasitology, 8: 88–100.

Hopkins, G. H. E., 1942. The Mallophaga as an aid to the classification of birds. Ibis: 94–106.

Rensch, B., 1924. Das Dépérétsche Gesetz. Z. indukt. Abstamm.- u. Vereblehre. 35: 139.

Wetmore, A., 1922. A study of the body temperature of birds. Smithson. misc. Coll. 72 (12): 1.

—— 1940. A systematic classification for the birds of the world. Smithson. misc. Coll. 99 (7): 1–11.

# Study of Bird Migration 1938—1950

*Rudolf Drost*

*Vogelwarte Helgoland, Wilhelmshaven*

## Contents

I. *General* .......................................... 216–217
General works.—Methods of study.—Stations and institutes.
II. *The Features of Migration* .......................................... 217–223
Routes.—Directions.—Times.—Wintering.—Difference concerning age and sex.—Flight.—Other migratory movements.—Invasions.
III. *Meteorological Factors* .......................................... 223–224
IV. *The Physiology of Migration* .......................................... 224–226
V. *Orientation* .......................................... 226–230
VI. *The Origin of Migration* .......................................... 230–231

The number of papers on bird migration, published in the last twelve years, is so great that it is impossible to consider all of them, apart from the fact that I was not able to see them all. When I agreed to give this lecture, I did not realize, how much more difficult it is to obtain ornithological periodicals than it used to be. I think, however, I have seen the most important of them—though possibly only as reviews—and therefore am able to give you an appreciation of the whole subject.

Bird migration is such a comprehensive and many-sided study, that in forty-five minutes only a very brief review can be given. Since the studies themselves and their results are the most important thing, we shall only allude to organization, methods and other general matters.

## I. General

General Works. Books on bird migration are to be found in many countries, by Salomonsen, Lincoln, Toschi, Thomson, Berlioz, van Oordt, L. Tinbergen, and additional general publications have appeared by Dupond, Putzig, Bonelli, Hardy, Roomval, Cathelin, Lincoln, Stimmelmayr, Griscom, Watson, Willet, Verheyen, Tugarinow and others.

Methods of Study. Experimental work is especially important as we see in the last part of this review, but one cannot exclude the old methods of field work, observation and ringing. Organized work by both methods has been done in many countries. Concerning ringing activities Dr. Rydzewsky is about to publish a detailed report, the first part of which is in the press.

New methods comprise observations by radar, the trapping of geese with rocket nets (P. Scott), and the ringing of ducks with wing marks (in Sweden and Finland).

There is no time to speak of ringing results, the method of publishing the recoveries, the terminology and so on.

Stations and Institutes. It is useful for the studies of bird migration that in most countries special institutes and organizations exist for the study of ornithology and migration, and that new institutes and bird observatories have been established. A most successful one is that at Ottenby on Öland, about which we shall be glad to hear details.

## II. The Features of Migration

### *The Paths of Migration*

Instead of "path" the terms "flightline" and "route" may be used, but the latter must not be considered in Palmén's narrow meaning as a "restricted" or "definite migration route." Välikangas having examined Palmén's theory with reference to bird ringing concludes from the evidence of his own researches, regarding migratory routes (in German "Zugstrasse") of the water and shore birds, that this need not be essentially changed. Passerine birds migrate mostly on a broad front though sometimes concentrated on small routes by "guiding-lines" such as coast, rivers, mountains, borders of woods (for instance for Chaffinches). This is confirmed anew by the papers of many authors, especially by the studies of ornithologists in the Netherlands and Finland. When two guiding-lines meet at one point, as for instance in the Bay of Wiborg, this will act as a funnel ("funnel-migration") and the number of birds may rise greatly to millions of ducks, as is the case at Wiborg (Putkonen).

In order to understand the distant migration of the Arctic Terns it is useful to know that they follow routes over cold waters of high biological productivity (Kullenberg, 1946).—Among new examples of species, which migrate along old routes of immigration, may be named the Golden Oriole (*Oriolus*, Stresemann, 1948).

B. Öhrn (1946) has made known a route for waders across Sweden along the Roxen-, Tåkern-, Vätter- and Bolmen lakes, which he presumes to be a relict of the migration route dating from the time when the fringe of the ice lay along that line.—Ringing results of passerine birds gave both examples of their taking the same route or choosing another one a great distance away. It also happens that a particular species takes a new route, as for example the Blue Goose (*Chen chaerulescens*) in the Mississippi Flyway (Hodges, 1948).

Many papers deal with migration at sea of oceanic birds (Bourlière, Roberts, 1946 and others), water- and landbirds as a result of watching and ringing. Ringing results brought new proofs of the crossing of the Atlantic (Arctic Tern, *Sterna macroura*, Hawksley, 1949; Kittiwake, *Rissa*, May Cooke, Dementieff etc.).—Lowery gave new direct evidence of a non-stop flight across the Gulf of Mexico, 500 miles over water and entailing moreover 24 hours or more of continuous flying. Still greater is the performance of some Indian birds (*Merops, Falco*), which migrate regularly to Africa in a non-stop flight of about 2500 km, entailing even in favorable conditions about 30 hours flying.—For other birds evidence exists of a "Schleifenzug" that is to say different routes in autumn and spring: *Oriolus*, Golden Oriole (Stresemann), *Muscicapa hypoleucos*, Pied Flycatcher (Drost and Schillings, Mayaud) and *striata*, Spotted Fl. (Creutz) and so on, but more noteworthy is that of the Black-throated Diver, *Colymbus arcticus*, from Russia and Siberia, which migrates by the direct route in the autumn and deviates in the spring (Bodenstein und Schüz).

### *Direction*

Observations of the direction of migration are important and have always been so, with regard to routes, meteorological factors, the physiology of migration, the behaviour of birds and last but not least to the problem of orientation.

Important work concerning the observation of directions is carried out especially in the Netherlands (L. Tinbergen, van Dobben, Makkink, Kluijver and van der Starre, Vleugel and others) and Finland (by von Haartman, Bergman, Koskimies and so on) and also in Sweden (Svärdson and others), which illustrated several cases of different directions.

A survey of the theoretical side is given by Geyr von Schweppenburg (1949). He proposes a new system with a new terminology. The "standard-direction" (= Normal-richtung), which the species possesses as a result of an inner urge, he now names "Primärrichtung" (primary-direction). He defines in addition three other directions, the "Sekundärrichtung,"= Taktische Richtung (= secondary-direction= tactile stimulus-direction) which implies a direction taken as a consequence of external influences such as guiding-lines and wind. The "Tertiärrichtung" (= tertiary-direction) —the direction established under the influence of the ability to return to a definite place, and lastly the "Quartärrichtung" (quarternary-direction, displacement-direction), taken by birds forced by drift of the wind. Geyr himself, however, speaks of these terms as a "preliminary system" only realizing the difficulties involved.

Reference must now be made to migration in false directions and reverse migration, the causes of which can be quite different. Reverse migration in spring (German "Rückzug") as a consequence of an irruption of cold is observed in most years, both in the Old and in the New World. Swanberg (1948) in one case assumed a psychological influence, not the consequence of lack of food, which is evident by the observations of the reviewer, who observed the change of the direction on the same night on several occasions years ago. The psychic causes of such reverse migrations, which are released by meteorological factors, are emphasized by Bergman (1949). The directions, he points out, are determined by two different tendencies, flying back and flying against the wind.—Dahl (1938) reports one strong reverse migration (caused by cold), by which Lapwings (*Vanellus*), which were already choosing their breeding places, were not influenced by the migration of mates of the same species; Oyster-catchers were also uninfluenced by the migration whereas the Ringed Plovers, which had already chosen their breeding place, disappeared and returned only three or more days later. The "randtrek" or "border migration" of Vleugel (1948) will be referred to in connection with meteorological factors.—A more noteworthy reverse migration is in the autumn, and is dealt with in a series of papers by von Haartman, Bergman, Koskimies. The essential point is that there is not only an influence on the direction caused by external factors, namely the physiognomy of the environment and the weather, but also inner factors, psychical or physiological, by an uncertainty in the urge to migrate. Such reverse migration, which is also found inland, takes place chiefly in the first stage of the migration of the species (for instance the Wagtail, *Motacilla alba*) and in a certain rhythm of the day. The authors assume a conflict between the urge to migrate and the urge to stay at home in these reverse migrants, which in the morning migrate and then return. As Koskimies observed, the reverse migrants are primarily young birds.—The anemotropotaxis can be observed in all years.

There are, moreover, cases of reverse migration of birds after ringing which may be psychical influences (Drost, 1949, perhaps also W. P. Smith, 1942).

## *The Times of Migration*

The symmetry of times ("Zeitsymmetrie") of bird migration engaged the attention of Hausl (1940), Geyr von Schweppenburg (1943) and others. All migrations between spring and autumn, between "home-migration" and departure or autumn migration can be classified as interim-migration (Zwischenzug). They can be quite different and further investigation is necessary. For instance, many species in the Rocky Mountains regularly move to higher altitudes in mid and late summer after the completion of nesting, presumably young birds but also adults of some species.—Interim-migration usually differs from and often is in the reverse direction to the autumn migration. It seems to occur in many more species than was assumed formerly, even in small birds.—The "weather-flight movements" (Koskimies, 1950) of the Swift, *Micropus apus,* cannot be considered as migration.—For the theory of interim-migration see Kraak, Rinkel and Hoogerheide (1940, 1942) and Geyr v. Schweppenburg (1943). "Moult-migration" (in German "Mauserzug," in Dutch rui-trek) is recorded in ducks (Stresemann, 1940), also for the Sheld-Duck (Hoogerheide and Kraak, 1942, Coombes, 1949), while Lapwings after their early summer migration make a moulting halt in the Netherlands (Klomp, 1946).—Here we may mention two papers by Kipp, concerning migration and breeding biology and the moult, and further concerning migration and wing form.—We can omit here autumn migration and winter movements (weather movements, "Winterflucht").—The time of spring migration is the subject of a series of papers (Stresemann, 1947, 1948, and others). Some authors studied the isochronal lines of the arrival, for instance Southern for 5 species, 1938–1941, Strautzels 1938 and Slivinsky 1938.

The rhythm, yearly and daily, is also a factor in the physiology of migration, but we shall here mention field observations, especially of Finnish ornithologists (see above), which are of great interest. There are also further observations of daily rhythm, by Franz, in the arctic winter (1943). Much has been written about migration at night, at lighthouses and so on. It should be defined we think, why and at what rate some birds migrate both by day and by night.

## *Winter Areas and Winter Habits*

Much work has been done in many countries concerning winter populations and biotops and concerning the winter habitats of single species. In America it was described as "a historic milestone in bird banding" that the winter home of the Chimney Swift was discovered in Peru (Lincoln, 1944).—The Arctic Tern winters in great numbers in the pack-ice zone, between 63° and 64° S. (Bierman and Voous, 1950, also gave interesting data about the migration in the Antarctic).—Reports concerning winter habits are given by J. Steinbacher (1938, re song), Büttiker and Braun (1941, re food), Wallace (1941, on habits of ringed Chickadees), Wing (1941, size of flocks), Krätzig (1943, association), Broekhuysen and Meiklejohn (1943, palaearctic waders and European Swallows in the Cape Peninsula), Ottow (1949, invasion of wood birds in the cold tundra), and others. —Here also can be mentioned the known winter movements of certain species, studied by Vleugel (see below).

It is an exciting fact that there is actually a winter sleep in birds, which really should migrate to warmer winter quarters. The hibernation of the Poor-Will, *Phalaenoptilus nuttallii,* a nighthawk of California, in a state of profound torpidity, has been proved even in the case of the same ringed bird during three successive winters (Jaeger, 1949, and others). In this connection the most interesting information has been forthcoming in the various reports of torpidity in birds, especially Swallows and Swifts (Mennig, 1940, McAtee, 1947 and others), and Humming-birds (J. S. Huxley, 1939).

## *Differences concerning Age and Sex*

It is necessary in the study of migration to examine in detail any species in question, if differences in age and sex are involved. This is stressed by Lincoln (1939), who reports on a "Symposium on the Individual vs. the Species" engaged also in the differences in migration of age and sex. The well-known migration order (in spring the first arrival of old males, then old females and young) is confirmed in many cases but there are also other conditions. Van Dobben and Bruyns examined birds killed on lighthouses and found that adults migrated on the average somewhat earlier than the young, for example Skylarks (*Alauda*) and some species of thrushes.—In *Chordeiles minor,* a nighthawk in Northern Idaho, females arrive on the breeding grounds some days before the males (Rust, 1947).—Lack, in his "Problem of Partial Migration," 1943–1944, points out that in all partial migrants females and young show a greater tendency to migrate south.

In his intensive examination of Chaffinches Deelder (1950) notes: differences in the autumn migration routes of males and females; in winter a surplus of males in Scandinavia, Holland and South England, but in Ireland a surplus of females, and further interesting facts. Amongst other papers dealing with sex ratio may be mentioned that of McIlhenny (1940).

## *The Flight*

In this short lecture we cannot examine the technique of flight, though it also has a bearing to some extent on migration. The use of thermal currents by birds in migration is the theme of several papers (Bergman, 1938, Wagner, 1941, Goodwin, Mackintosh, both 1949).—Poncy reports on triangular formations, Geyr deals with association (1949).

Height and Speed: Different methods for measuring the height of migrating birds are recommended, by L. Tinbergen and by Bergman and others. The best method is, of course, with a rangefinder, as used for military purposes. By this method Sinding (1947) observed Corvidae and pigeons not higher than 300–400 m, birds of prey 600–800 m, while the Common Buzzard, *Buteo buteo,* reached in one case 1200 m. In the same way Common Cranes, *Grus grus,* were seen gliding 2960 m high in a thunderstorm and with the speed of 55–60 m/sec. Long-tailed Ducks, *Clangula hyemalis,* and Common Scoters, *Oidemia nigra,* migrate near Helsingfors mostly at a height of 500 to 800 m, sometimes at 930, 1050 and 1220 m; these heights were measured exactly by two observers by trigonometrical methods (Bergman, 1941). There are still too few exact observations on speed of flight; information about the wind is always necessary as Allen states (1939). It is to be hoped that exact observations may be made by means of radar.—The speed of migration is reported in many papers on recoveries of ringed birds by Miss May Cooke (1940) and others. Some of the highest speeds average 410 km per day (Redstart, Buxton), 440 km (Starling, Drost and Grittner), 438 km or may be 730 km in one night (Coot, *Fulica atra,* Müthel).

## *Other Movements*

The Atlantic Murre (or Guillemots) regularly swim to their winter areas (Johnson).—Bergman observed migrant Brent Geese, *Branta bernicla,* swimming on the Finnish coast 12 or 13 km in one day.

## *Invasions*

The research work of the last years has increased our understanding of what we call "invasions" or "irruptions" namely the irregular movements of some species such as the Waxwing, *Bombycilla,* Snowy Owls and others, and has increased our knowledge about the problems of migration as a whole. It is now evident that an "irruption bird" such as the Waxwing also undertakes long range movements influenced by an inner urge to migrate, as does the true migrant. (Siivonen, 1941, and van Oordt, 1950). Kalela, who studied the problem of invasions most intensively (1944, 1949), writes that "the limit between invasion and autumn migration is undoubtedly very diffuse." A review of the new publications about cyclic mass productions in birds and small mammals is given by Franz (1950). The opinion of Kalela is briefly: the irregular migrations of animals are adapted in a high degree to sudden fluctuations of the environmental conditions. Great invasions arise, if the population is increasing especially heavily and the lack of food affects a wide area. Kalela further suggests the possibility that great irregular migrations may have played a part in the development of ordinary seasonal bird migrations.

Much has been published concerning the irruptions of single species, of which there is no time to speak. We will mention only some voluminous works about the Waxwing, *Bombycilla garrulus* (Warga), the Crossbill, *Loxia curvirostra* (Kirikow, 1940), the Jay, *Garrulus glandarius* (Putzig, 1938), the Rough-legged Buzzard, *Buteo lagopus* (Schüz, 1945) and the Snowy Owl, *Nyctea nyctea* (Gross, 1947).—Ritchie (1940) has shown that the invasion of Waxwings in 1921 was much influenced by weather and especially by barometric pressure.

## III. The Meteorological Factors

Meteorological factors in their widest sense are important to some extent in connection with many problems of bird migration, for example direction, migration time, flight, invasions, as you have heard, but they also touch further questions of physiology and orientation and last but not least the origin of migration.

In addition to the climatic and the weather factors, we must also consider astronomic or cosmic elements, e. g. the sun whose influence may be indirect, or as some suppose, direct. In studying the influence of meteorological factors on bird migration we have to distinguish, whether it concerns migration as a seasonal phenomenon, or the start of every single migration period or the behaviour of the birds during migration, that is to say flying and resting. Vleugel believes that the weather movement in spring, in German "Rückzug," is the same as his "frost-flight" in winter. He distinguishes another weather movement: the "border migration," in a northeasterly direction, caused by rising temperatures, most frequently after frost periods (with "frost flight").—The mass departure of Chaffinches in a reverse direction after a snowfall in spring is caused—writes Bergman (1949)—by psychical and released by meteorological factors.

We shall consider later, if the initiation of true migration is due in part to weather conditions.

Many papers deal with individual weather factors, temperature, wind, barometric pressure, weather fronts, air-electricity and so on, but we cannot mention them all.

Southern showed in his studies of spring migration that the correlation between isolines and isotherms is not the same for any one species and is absent in the Red-Backed Shrike, *Lanius collurio.* Many authors confirm a correlation between departure, passage, and arrival, and the falling or rising of temperature; but we must emphasize the great variety concerning birds (species and populations), and regions, not only in this connection but in all problems of bird migration.— The influence of wind with regard to routes and the height has been studied particularly in the Netherlands (L. Tinbergen and others), and also in other countries.

Concerning barometric pressure we will in the main consider the recently published paper by Bagg and others (1950) in U. S. A., and the relative literature referred to therein. They state inter alia "that, during the period of spring migration, pronounced movements take place into or through a given region during the time between the passage of a warm front through that area and the subsequent arrival of a cold front." This agrees, on the whole, with similar statements by other authors with regard to the relation between barometric pressure patterns and migration, but it is still a question as to what is the determining factor, and if it is barometric pressure itself. A very interesting instance was reported by Schüz in the case of two Rough-legged Buzzards avoiding a bad weather front. Palmgren and his school indicate that probably air electricity plays a decisive part.

The climate, i. e. average weather, has recently changed in northern and central Europe, which has affected the avifauna too; some typical migrants, summer birds, are decreasing in like measure with the decrease in summer temperatures and increased rainfall, whereas other migrants, which return early in the spring, show an increase and expansion comparable to the warmer winters and springs (Kalela, 1949 + 1950, and others).

## IV. The Physiology of Migration

The chapter "physiology of migration" has to deal in the main with the internal factors which influence birds, the rhythms, the urges, the stimuli, and in particular the connected experiments. This concerns firstly typical migrants, named formerly by Weigold "Instinktvögel" and by Putzig (1939) "Innenweltbedingte Zugvögel" and 1948 by Vleugel "introverse trekvogels" or "introvert migrants." The opposite are weather migrants, "ausserweltbedingte Zugvögel," "extrovert migrants."

Observation in the field and experimental work have proved meteorological factors are only of secondary influence. The primary factors lie within the birds themselves. In searching for these, much experimental work is done with cage birds.

Palmgren has pointed out that the daily rhythm in birds is an important factor in migration and that its study is necessary to understand the mobility of caged birds as recorded by actographs.

Palmgren and other Finnish ornithologists have published valuable contributions about diurnal rhythms. The intensity of activity of cage birds, both of those which migrate by day or night, corresponds closely to what has been observed in nature. This justifies the conclusion that the actograph records reflect essential points of the physiology of migration.

The main point of these studies confirms that birds have fixed daily rhythms these determine the times of day or nocturnal migration, of rest and sleep and so on. Thus: "The nocturnal migration flight is as a rule carried out in the earlier part of the night," whereas "the birds which migrate in the daytime perform their wandering almost exclusively in the morning hours" (Palmgren, 1949).

Research of the factors causing migration concern in the main, apart from the environmental factors, metabolism, the endocrine system and the length of daylight.

Metabolism has been studied by Merkel and Putzig and others, but further work is necessary.—The significance of fat deposition and of weight is described by many authors (for instance Wolfson, Bont, Baldwin and Kendeigh, Mrs. Nice, Schüz, Shaw, Stresemann and by others).

A large number of writers, especially in North America, studied endocrinology in connection with bird migration, viz. Schildmacher, Stadie, Putzig, Merkel, Gal, Hann, Rowan, Wolfson, Rollo, Miller, Burger etc. and most of them concentrated in the main on the sexual cycle and the influence of light or length of daylight upon the gonads. The researches of Rowan and others suggested as an alternative that it is light as light, which effects the evolution of the gonads, or the activity caused by length of day.—The fact that the gonads are not decisive factors is proved by migrations of castrated birds.—Wolfson states that both alternatives may be right. He assumes the following: "As the days increase in length, birds are awake for longer periods of time because the state of wakefulness, at least in some birds, is a response to light; the concomitant activity of the hypothalamus causes an increased production or release, or both of the gonadotropic hormones from the anterior lobe of the pituitary; those in turn, stimulate gonadial recrudescence." Moreover the hypothalamus "plays a part in fat metabolism" and it seems to be that organ of the nervous system which determines breeding and migration time. Rowan speaks too of the meaning of the hypothalamus, but he supposes that the gonads, activated by the pituitary glands, may initiate migration. Burger 1949 concludes: "the theory, that light acts indirectly by promoting increased hypothalamic activity through longer bodily activity or wakefulness, stands not proven." Thus we are, remote from a commonly acknowledged theory still less from a solution of the problem. Nevertheless we will consider the Wolfson's assumption concerning the causes of migration. He maintains that the regular change of day length (external factor) over a long period of time makes the birds respond to the internal factors namely: the growth of the testes, the increase in the secretory activity of the pituitary gland, the heavy deposition of fat and the concomitant increase in body weight to a maximum. "The physiological response of the bird eventually reaches a state that will enable the bird to meet the energy requirements of migration. Then, the behaviour patterns which initiate the migratory flight are released.

The cyclic nature of the secretory activity of the endocrine system is regarded as an inherent rhythm, since it is a result of the heritable properties of the glandular tissues. The inherent rhythm, however, is not regarded as being automatic or spontaneous, but is under the direct influence of the external environment in causal relationship."

## V. Orientation

No less difficult and interesting is the problem of orientation, which to quote Thomson is twofold, firstly: "what factors determine the path and goal of any particular migration?" and secondly: "how do the birds find their way by that path to that goal?" It is obvious that in our short survey of bird migration we have to pass quickly over this very complex and difficult problem.

Of the authors who published reviews on orientation, apart from those who wrote a general work about bird migration, such as Thomson and others, we shall include van Oordt, van Dobben, Daanje and Kluijver (1940), Koehler (1942), Griffin (1944 and later), von Haartman (1947), Salomonsen, Verwey and Deelder (1949). Here may be mentioned "a discussion of the orientation of birds on migratory and homing flights," published by the Linnean Society of London 1949.

The ability of migrants to find their way home in spring (named "Ortstreue") and to the same place in winter ("Winterortstreue") is known and proved by many new instances.

L. Tinbergen (1941, 1949), discussing the "preferred direction" which the birds choose when they are not directed by the configuration of the landscape, gives interesting suggestions and ideas. The birds correct—he points out—the drift of the wind in selecting their aiming points. They fly low in bad visibility, because they are not otherwise able to view two points one behind the other. The Chaffinches cease flying over the coast at sea with a side wind, because there are no fixed points at sea. Inland the correction of the drift can be troublesome, when the direction and the force of wind is inconstant. Therefore few migrants are found in such weather. So far L. Tinbergen.—Palmgren (1939) assumes, that deviations from the normal direction in mass migrations during weather front passages, and the change of direction in greater areas are caused by factors decisive from that direction, this may be perhaps the electric potential between air masses of different charge.

In migrating birds sight is important without doubt. This is shown by the observations of night-migrations at lighthouses and so on. Williams points out that it is obviously vital for migrating birds to be able to land safely whenever they wish.—By day movements of birds are often seen, soaring or flying in spirals. This seems to be used for orientation (Woodcock, 1940, Waterhouse, 1949). Svärdson, having observed gyrations by migrating gulls, does not agree with this opinion and suggests that gyration is the parallel double response to different impulses as the bird is flying but yet stationary.—The statements of Miller (1941) are very interesting: Two Lincoln Sparrows caught during spring migration were liberated at seven p. m., some minutes after the sun had set, one after the other. Both of them flew at first in a southeasterly direction, the only one possible from the balcony of the house, but then they suddenly returned, high over the house, in the correct northwesterly direction.—There are further noteworthy observations which cannot be dealt with in this short time.

A great deal of experimental work has been done to elucidate the orientation problem. Carrier pigeons are not migratory birds, but we have to deal with them also. The literature about their homing ability is voluminous. The last word has not been spoken. By now we have to assume from the results of Oskar and Käthe Heinroth (1941), that the homing ability in pigeons depends on the sense of sight and that they spiral in unknown regions until they find a familiar landmark. The experiments of Platt and Dare (1945) confirm, that homing in pigeons is dependent on the recognition of familiar landmarks.

The further experiments with sedentary birds (Creutz, Schifferli and others) prove that these wild living birds too are unable to find their way home from unknown regions over a greater distance. But the Goshawk (*Accipiter gentilis*) which is a sedentary or vagrant bird (with a winter territory of up to 100 km in diameter) returned from distances of 300 and 600 km (Rüppel, 1940, 1948).

In many papers the "homing instinct" of transported breeding birds is reported. Among these the systematic investigations by Polish ornithologists (Wojtusiak and Ferens, Wodzicki, Puchalski and Liche), by Lack and Lockley, Schifferli, Rüppell and Griffin are of importance. It is noteworthy that Starlings, newly hatched and caged for one year, could not find their way back from a distance of 114 km, whereas old birds, caged for one year, were able to return (Rüppell, 1938, 1941). The most important of the several experiments made by Griffin (together with Hock) is that with Gannets, released inland and followed by aeroplane. The observations indicate that the birds in unfamiliar territory performed more or less random movements until a familiar area (coast line) was encountered. This is similar to the behaviour of an inexperienced Carrier pigeon, but we must point out, that Gannets are not migrant birds, though Griffin in his experiments with the Common Tern suggests that these birds behave in the same manner. It is essential to appreciate that homing was very slow, when the birds were transported only 15–25 miles. This agrees with the results for Swallows in Poland, that the homing speed increases when they are transported farther away even up to 100–150 km.—Wojtusiak in his last paper (1949) reports that the transported Swallows on release always flew in circles and then disappeared in a certain direction. He further reports on experiments with infra-red rays (which may be of special interest).

We now mention the transport of young birds, not yet flyers or even as eggs. Mallards bred at Rossitten from English eggs behaved—as did English mallards bred in Finland—as the ducks in their new home, but it is not certain they were not influenced by other ducks (Putzig, 1938). Sheld-Ducks, bred by Schifferli from eggs from the Isle of Sylt, North Sea, settled in Sempach, Switzerland. We think that the recovery of one Sheld-Duck on the shore of the Baltic Sea is not enough to prove an inherent instinct towards their proper home, to the home of the egg. Experiments with young birds show the same result: they do not return to their proper home but to the place where they have grown up and were liberated (Packard, Mc Cabe, 1947, Schüz, 1942). The best example is the case of Common Gulls transported from the Baltic Sea inland to Silesia, where they were found breeding some years later, though they do not usually breed inland (Stadie, 1938, Krampitz, 1941). In this connection we understand better why Rüppell's young Starlings after a year of captivity and without being liberated could not find their way home (see above). We think that young birds feel "Ortstreue," the desire to go home, only to that place, with which they have become acquainted after being fledged or released.

Amongst the displacement experiments on birds caught during migration, those of Rüppell (1944) and Rowan (1946), with crows, *Corvus cornix* resp. *brachyrhynchos* are of especial interest. In both cases transported birds migrated in the normal direction but with a parallel displacement corresponding to their transport. Both authors feel justified in speaking of a "sense of direction." It may be mentioned that the crows in question were young (all *brachyrhynchos* and most *cornix*) and we can compare this with the behaviour of young Sparrow Hawks transported from Heligoland to Silesia and migrating to Italy. It would be very important to carry out such transportation with typical migrants during migration.—Schüz himself will demonstrate to us the interesting experiments of the Vogelwarte Rossitten, so I will say no more about this (p. 249).

Some authors made experiments with caged birds. Dijkgraaf (1947) found that none of his birds could appreciate the direction "south" and concludes that they responded only to visible or audible stimuli. He suggests orientation over the ocean by direction of wave fronts and by sun position over land. The experiments of Kramer (1949, 1950) are most important. He found that the observed tendencies of direction of his caged birds are the direct expression of orientation in migration. He himself will tell us more about his results (p. 269).

We have still to mention that there have also been anatomical investigations concerning the possible place of a hypothetic sense organ, namely by Werner, Palmgren, Steinhausen, Pumphrey.

It will be useful to consider proximate orientation for judging distant orientation. As an example may be mentioned the study of von Haartman of the Pied Flycatcher (1947), which confirmed the birds' capacity for learning in comparison with mammals.

It is useful as well to consider the orientation of other animals. Naming the papers of Lotze (1940), Baerends (concerning Ammophila, an earth wasp), von Frisch (1946, conc. the bee), Neuhaus (1948, conc. mice), Verwey (1949, conc. fishes).

So much for the general facts. Now we will consider the theories about bird migration. Most people acknowledge the capacity of migrants to take a certain direction, some assume a "sense of direction" (for instance Rüppel, Rowan, Verwey, Deelder) and some a "sense of geographical position." The physiologist O. Koehler refuses to accept such senses and so do others such as Griffin. The fact is that migrant birds have the tendency and the ability to take a certain direction, typical for the species or the population, as we know from experiments by Schüz and others with transported birds and by Kramer with caged birds.—The inherited knowledge of the geographical position of the home cannot be assumed in the case of experiments with young birds or eggs.

The ability to take the direction must be supported by one or more external factors. It may be that the earth's magnetic field with its components can assist bird navigation but up to now nobody can show in what manner. Interesting hypotheses have been presented by the Physicist Ising, concerning the earth's rotation, the Coriolis force, and of Yeagley, concerning the vertical component of the earth's magnetic-field and concerning the Coriolis force. The following discussion (of Thorpe, Slepian, Varian, Davis, Savile, Henderson, Allen, Griffin, Kramer, Schumacher, Wilkinson) resulted in a failure to agree on the main points. It could not be accepted that birds are able to perceive the very small differences in the magnetic field and of the Coriolis force.—Possibly bird navigation is simpler than we think, concerned mostly with known external factors, or on the other hand with visual recognition as is assumed, for instance, by Thomson and Wynne-Edwards. Some authors believe the position of the sun to be the guiding factor (Rüppell, Griffin and others). The latter suggests as clues for the birds: 1) the direction of sunrise, of sunset, or of other celestial landmarks and known geographical features, 2) typical air masses, the prevailing winds, 3) ecological clues.—Perhaps there are other factors not yet known. We do not suggest that birds are guided by waves, if we mention the fact, that migrants show a positive reaction to ultra-shortwave (radar) transmission (Drost, 1949); we shall only mention that birds are able to react in cases where men are not able to do so.

We will not finish this section without mentioning the importance of psychic factors. Bird migration is not a "chemical reaction," which always takes the same course. The fact that the psychic condition is essential in many cases and in most features of migration, also in orientation, is pointed out in papers by Geyr, Drost and others.

## VI. The Origin of Migration

Some final remarks on the origin of migration. Wolfson (1948) proposes the hypothesis that many of the intercontinental migratory and oceanic routes can be explained by assuming a gradual separation of breeding and feeding areas as the result of the continental drift. Objections to this hypothesis are presented by Amadon, especially concerning the incompatibility in time, this is also pointed out by Schüz in his review (Vogelwarte 15, 1, 1948, p. 54). Some further authors partly deal with the origin of bird migration, as Mayr, Woodbury, Kullenberg, Landsberg, McAtee, Paige an others. We may suppose that bird migration could originate at any time, if the appropriate conditions apply and the species in question has the necessary plasticity; this could not occur suddenly but over a long time. If the young of sedentary birds, transported to a region with a severe winter climate, would fly away to warmer areas, this would be a noteworthy weather movement and perhaps the first step towards true migration. We do not know, if the migrations of English mallards, transported as eggs to Finland and Rossitten, can be considered in such a manner; in any case further experiments with definitely sedentary birds should be carried out.

My review has shown that the progress in the study of bird migration made in the last twelve years is remarkable, but that there are still a number of problems to be solved. We must admit that field work is as necessary as ever, especially if modernized and carried out in conjunction with other methods, but experimental work is the most important. It is possible that by the next International Ornithological Congress some decisive results may have been achieved.

*Discussion*:

J. S. **Huxley**: Dr Drost referred to the remarkable discovery in an American Caprimulgid of true hibernation, which made migration unnecessary. In my opinion the phenomenon of "temporary hibernation" or complete reversible torpidity and poikilothermy in humming birds, and to a lesser extent in Colies,[1] is a similar adaptation, permitting these small-bodied birds to extend their breeding ranges to areas with colder nights which would otherwise prove fatal. It is probably no mere coincidence that these birds and the nightjars are all related.

G. **Kramer** fragt nach weiteren Fällen, in denen gerichteter Zug durch andere motorische Mittel als durch Flug zustandekommt. Ausser dem von Drost zitierten Fall (*Uria*) sind ihm noch die über die Windenburger Ecke wandernden Rebhüner (*Perdix perdix*) bekannt, die bis zu ihrer Ankunft am Wasser zu *Fuss* wandern (von *Posingis* beobachtet). Ferner scheinen Stare (*Sturnus vulgaris*) während der Ruhestunden vorwiegend in Zugrichtung zu marschieren während sie Futter suchen.

E. **Schüz**: Es gibt eine Literaturstelle, dass *Fulica americana* Zahlreich in Zugrichtung wandernd beobachtet worden ist.

---

[1] Huxley, T. S.; Wells, C. S., and Best, A. T., 1939., Nature 143: 683.

## References

A Discussion of the Orientation of Birds on Migratory and Homing Flights, 1949; Proc. Linn. Soc. London 160, Part. 2: 85–116.

Allen, W. H., 1948. Bird Migration and Magnetic Meridians; Science 168, 281: 708.

Amadon, D., 1948. Continental Drift and Bird Migration; ibid. 108, 281: 705–707.

—— 1949. Comments on Recent Literature (about hibernating birds); Wilson Bull. 61: 237–238.

Austin, O. L., 1948. Site tenacity, a behaviour trait of the Common Tern (*Sterna hirundo* L.); Bird-Band. 20: 1–39.

Bagg, A. M., Gunn, W. W. H., Miller, D. S., Nichols, J. T., Smith, Winnifred, and F. P. Wolfarth, 1950. Barometric Pressure-Patterns and Spring Bird Migration; Wils. Bull. 62: 5–19.

Baerends, G. P., 1941. Fortpflanzungsverhalten und Orientierung der Grabwespe *Ammophila campestris*; Tijdschr. Ent. 84: 71–75.

Baldwin, S. P., and S. Kendeigh, 1938. Variations in the weight of birds; Auk 55: 416–467.

Bergman, G., 1941. Der Frühlingszug von *Clangula hyemalis* und *Oidemia nigra* bei Helsingfors. Eine Studie über Zugverlauf und Witterung sowie Tagesrhythmus und Flughöhe; Orn. Fenn. 18: 1–26.

—— 1938. Auffallender Raubvogelzug unter der Einwirkung von steigenden Luftströmungen; ibid. 15: 107–111.

—— 1948. Sträck, återflygning och övernattning hos sädesärlan (*Motacilla a. alba* L.) under hösten vid Ölands södra udde; Vår Fågelvärld 7: 57–67.

—— 1949. Om bofinkens, *Fringilla coelebs* L., vårsträck i Helsingforstrakten i relation till väderlek och ledlinjer; Orn. Fenn. 26: 43–57.

Berlioz, J., 1942. Les migrations d'oiseaux; Les migrations animals, Paris (L'avenir de la science, 17 Gallinard): 91–162.

Bierman, W. H., and K. H. Voous, 1950. Birds observed and collected during the whaling expeditions of the "Willem Barendsz" in the Antarctic 1946–1947 and 1947–1948; Ardea 37: 123.

Bodenstein und Schüz, E., 1944. Vom Schleifenzug des Prachttauchers (*Colymbus arcticus*); Orn. Mber. 52: 98–105.

Bonelli, G., 1939. Precisazione delle Migrazioni e nuova interpretazione dei passi. La respirazione impulso migratorio?; Riv. Ital. Orn. 9: 178–197.

Bont, A. F. de, 1947. Le métabolisme des graisses chez les oiseaux migrateurs et sédentaires; Gerfaut 37: 57–62.

Bourliere, F., 1946. Notes Biologiques sur les Oiseaux de l'Atlantique Nord; L'Oiseau 16: 42–60.

Broekhuysen, G. J., and M. F. M. Meiklejohn, 1943. Observations on Palaearctic Waders and European Swallows in the Cape Peninsula; The Ostrich Suppl. No. 1: 38.

Burger, J. W., 1949. A review of experimental investigations on seasonal reproduction in birds; Wils. Bull. 61: 211–230.

Buss, J. O., 1946. Bird detection by radar; Auk 63: 315–318.

Büttiker, W., und R. Braun, 1941. Die Ernährung der überwinternden Wasservögel auf dem Klingnauer Stausee; Vögel der Heimat 11: 162–171.

Buxton, J., 1950. The Redstart; Collins, London 8: 180.

Cathelin, F., 1940. Le problème des migrations des oiseaux; Bull. Soc. Acclim. Fr. 87: 158–172.

Cooke, May Th., 1940. Notes on Speed of Migration; Bird-Band. 11: 21.

— — 1945. The Kittiwake as a Transatlantic Bird; ibid. 16: 58–62.

Coombes, R. A. H., 1949. Sheld-Ducks: Migration in Summer. The Intern. Wildfowl Research Institute. Publication No 1; Nature 164: 1122.

Creutz, G., 1941. Vom Zug des Grauen Fliegenschnäppers, *Muscicapa striata striata* (Pallas); Vogelzug 12: 1–14.

— — 1949. Untersuchungen zur Brutbiologie des Feldsperlings (*Passer m. montanus* L.); Zool. Jahrb. Abt. System. 78: 133–172.

Daanje, A., en H. N. Kluijver, 1940. Het orienteeringsvermogen van trekvogels; Tijdschr. Parapsychol.: 12.

Dahl, E., 1938. En rubbning i västkustens fågelsträck påsken 1937; Fauna och Flora: 69–76.

Danielsson, G., Edelstam, C., och G. Svärdson, 1947. Ottenby fågelstation, dess tillkomst och verksamhet, år 1946; Vår Fågelvärld 6: 38–51.

Davis, L. jr., 1948. Remarks on "The Physical Basis of Bird Navigation"; J. appl. Physics 19: 307–368.

Deelder, C. L., 1949. On the orientation of migrating animals; Bijdragen tot de Dierkunde 28: 503–504 (Addendum zu: Verwey, 1949, ibid: 477).

— — 1949. On the autumn migration of the Scandinavian Chaffinch (*Fringilla c. coelebs* L.); Ardea 37: 1–88.

Deelder, C. L., en L. Tinbergen, 1947. Waarnemingen over de Vlieghoogte van Trekkende Vinken, *Fringilla coelebs* L. en Spreeuwen, *Sturnus vulgaris* L.; Ardea 35: 45–78.

Dementieff, G.-P., 1946. Les migrations transatlantiques de la Mouette tridactyle, *Rissa t. tridactyla* L.; L'Oiseau 16: 37–41.

Dijkgraaf, S., 1946. Over het orientatieprobleem bij vogels; Koninkl. Nederl. Akad. Wetensch. 49: 690.

— — 1947. Über das Problem der Fernorientierung bei Vögeln; Österr. Zool. Z. 1: 314–324.

Dobben, W. H. van, 1939. Theorieën over vogeltrek en vogeltrek over Nederland. "Vogeltrek en Vinkenbaan": 1–8.

— — 1940. Oriëntatie bij vogels; Vakbl. Biol. Helder 21: 225–240.

— — 1944. Vogeltrek aan het Kanaal; Ardea 33: 1–22.

Dobben, W. H. van, und M. F. Mörzer Bruyns, 1939. Zug nach Alter und Geschlecht an niederländischen Leuchttürmen; Ardea 28: 61–79.

Drost, R., 1941. Zug einer kastrierten Amsel, *Turdus m. merula* L.; Vogelzug 12: 163.

— — 1949. Verkehrte Zugrichtungen als Beispiele einer "Zugscheu"; Ornithologie als Biologische Wissenschaft (Stresemann-Festschrift), Heidelberg: 255–260.

— — 1949. Zugvögel perzipieren Ultrakurzwellen; Vogelwarte 15, 2: 57–59.

Drost, R., und Ilse Grittner, 1942. Helgoland als "Brennpunkt" des Starenzuges; Ber. Ver. Schles. Orn. 2: 10–19.

Drost, R., und L. Schilling, 1940. Über den Zug des Trauerfliegenschnäppers, *Muscicapa hypoleuca* (Pall.); Vogelzug 11: 71–85.

Dupond, Ch., 1938. La migration des Oiseaux; Musée Royal d'Hist. Nat. d. Belgique, Bruxelles: 20.

Franz, J., 1949. Jahres- und Tagesrhythmus einiger Vögel in Nordfinnland; Z. Tierpsychol. 6; 309–329.

— — 1950. Zyklische Massenvermehrungen bei Vögeln und Kleinsäugern. Sammelbericht über neueres Schrifttum; Vogelwarte 15, 3: 141–155.

v. Frisch, K., 1946. Die Tänze der Bienen; Österr. Zool. Zeitschr. 1: 1–48.

v. Frisch, K., 1946. Die "Sprache" der Bienen und ihre Nutzanwendung in der Landwirtschaft; Experientia 2: 397–404.

Gal, G., 1939. (Zyklische Veränderungen der Schilddrüse der Vögel); Dissertat. Pannonhalma: 1: 64 (ungarisch m. deutsch. Zusammenfassung).

Geyr v. Schweppenburg, H. Frhr., 1943. Mauserzug-Zwischenzug; Vogelzug 14: 73–76.

—— 1943. Zur Zeitsymmetrie im Vogelzuge; ibid. 14: 112–113.

—— 1949. Zur Theorie der Zugrichtung; Ardea 36: 219–257.

—— 1949. Zuggeselligkeit; Ornithologie als Biologische Wissenschaft (Stresemann-Festschrift): 261–268.

Goodwin, D., 1949. Notes on the Migration of Birds of Prey over Suez; Ibis 91: 59–63.

Griffin, D. R., 1940. Homing Experiments with Leach's Petrels; Auk 57: 61–74.

—— 1943. Homing Experiments with Herring Gulls and Common Terns; Bird-Band. 14: 7–33.

—— 1944. The sensory basis of bird navigation; Quart. Rev. Biol. Baltimore 19: 15 31.

—— 1949. Die Navigation der Vögel; Naturw. Rundschau 2: 491–496.

Griffin, D. R., and R. J. Hock, 1948. Experiments in bird navigation; Science 107: 347–349.

—— 1949. Airplane Observations of Homing Birds; Ecology 30: 176–198.

Griscom, L., 1943/1944. The changing seasons; Audubon Mag. New York 45/46.

Gross, A. O., 1947. Cyclic invasions of the Snowy Owl and the migration of 1945–1946; Auk 64, 584–601.

Haartman, L. v., 1939. Über den Herbstzug von *Numenius a. arquata* (L.) und die Witterung, Orn. Fenn. 16: 52–67.

—— 1944. Die Orientierung des Trauerfliegenschnäppers, *Muscicapa h. hypoleuca* (Pall.), zum Nesteingang in einem Nistkasten mit mehreren Öffnungen; Orn. Fenn. 21: 69–89.

—— 1947. The proximate Orientation of the Pied Flycatcher, *Muscicapa hypoleuca* (Pall.), studied by the Multiple Choice Method; Soc. Scient. Fenn. Commentationes Biologicae X: 55.

—— 1945. Umschlagende Zugrichtung beim Buchfinken, *Fringilla c. coelebs* L., im Herbst; ibid. 22: 10–16.

—— 1947. Flyttfågelorienteringens Gåta; Nordenskiöld-Samfundets Tidskr.: 37–69.

—— 1949. Svartvita flugsnapparens, *M. hypoleuca* (Pall.) hemortstrohet; Vår Fågelvärld 8, 74–80.

—— 1949. Der Trauerfliegenschnäpper I. Ortstreue und Rassenbildung; Acta zool. Fenn. 56: 104.

Haartman, L. v., und G. Bergman, 1943. Der Herbstzug an zwei Orten in Südfinnland und seine Abhängigkeit von äusseren Faktoren; ibid. 39: 1–33.

Haartman, L. v., Bergman, G., und Koskimies, J., 1946. Beobachtungen über umschlagende Zugrichtung der Bachstelze, *Motacilla a. alba* L. im Herbst; Orn. Fenn. 23: 50–62.

Hamerstrom, F. N. Jr., and Frances Hamerstrom, 1949. Daily and seasonal movements of Wisconsin Prairie chickens; Auk 66: 313–337.

Hann, H. W., 1939. The relation of castration to migration in birds; Bird-Band. 10: 122–24.

Hardy, E., 1940. Bird migration; Quart. Rev. London 274: 219–232.

Hausl, N., 1940. Jahreswinkel und Lebenswinkel. Ein Beitrag zur Frage des Vogelzuges; 21. Ber. Naturw. Ver. Landshut: 33.

Hawksley, O., 1949. Transatlantic Arctic Tern Recoveries; Bird-Band. 20: 185.

van Hecke, F., 1946. Le Radar et ses applications en Ornithologie; Gerfaut 36: 20–27.

Heinroth, O., und Käthe Heinroth, 1941. Das Heimfinde-Vermögen der Brieftaube; J. Orn. 89: 213–256.

Henderson, G. H., 1948. Physical Basis of Bird Navigation; Science 107: 597–598.

Hodges, J., 1948. Some more Problems in Bird Migration; ibid. 108: 707–708.

Hoogerheide, J., und W. K. Kraak, 1942. Voorkomen en trek van de Bergeend, *Tadorna tadorna* (L.), naar aanleiding van veld-observaties aan de Gooise kust; Ardea 31: 1–19.

Huxley, J. S., Webb, C. S., and A. T. Best, 1939. Temporary Poikilothermy in Birds; Nature 22: 638.

Ising, G., 1945. The physical possibility of a biological sense of orientation based on the rotation of the earth; Ark. Matematik, Astronomi och Fysik 32 A: 1.

Jaeger, E. C., 1949. Further observations on the hibernation of the Poorwill; Condor 51: 105–109.

Johnson, R. A., 1940. Present Range, Migration and Abundance of the Atlantic Murre in North America; Bird-Band. 11: 1–17.

Kalela, O., 1944. Über den 10jährigen Massenwechsel bei pflanzenfressenden Vögeln und Säugetieren nebst einigen Gesichtspunkten zu seiner Erklärung; Orn. Fenn. 21: 42–62.

— 1949. Über Fjeldlemming-Invasionen und andere irreguläre Tierwanderungen; Ann. Zool. Soc. Zool. Bot. Fenn. 13: 90.

— 1949. Changes in Geographic Ranges in the Avifauna of Northern and Central Europe in Relation to Recent Changes in Climata; Bird-Band. 20: 77–103.

— 1950. Zur säkularen Rhythmik der Arealveränderungen europäischer Vögel und Säugetiere, mit besonderer Berücksichtigung der Überwinterungsverhältnisse als Kausalfaktor; Orn. Fenn. 27: 1–30.

Kipp, F., 1942. Über Flügelbau und Wanderzug der Vögel; Biol. Zbl. 62: 289–299.

— 1943. Beziehungen zwischen dem Zug und der Brutbiologie der Vögel; J. Orn. 91: 144–153.

Kirikow, S. W., 1940. Über die Beziehungen zwischen den Kreuzschnäbeln (*Loxia curvirostra* L.) und einigen Nadelhölzern; Bull. Ac. Sc. USSR (Biol.): 359–376.

Klomp, H., 1946. Verslag van het Kievitenringstation "Reeuwijk" over de jaaren 1943–1945 en gegevens over de trek van de Kievit; Limosa 19: 76–117.

Kluijver, H. N., en C. van der Starre, 1943. Verslag van het kievitenringstation te Reeuwijk over de jaaren 1938–1942; Ardea 32: 264–272.

Koehler, O., 1942. Zum Heimfinden der Tiere; Z. f. Tierpsychologie 5: 152–181.

Koskimies, J., 1947. (Wing marking—a new method for marking gallinaceous birds); Orn. Fenn. 24: 54–58.

— 1944. (Eine Rückzugserscheinung im Anfangsstadium des Herbstzuges bei der Bachstelze, *Motacilla a. alba* L.); ibid. 21: 65–69 (Finnisch mit deutscher Zusammenfassung).

— 1947. Über den Herbstzug der Bachstelze, *Motacilla a. alba* L. in der Gegend von Helsinki; ibid. 24: 61–79.

— 1950. The life of the Swift, *Micropus apus* (L.), in relation to the weather; Ann. Acad. Scient. Fenn., Ser. A, IV. Biol. No. 15: 1–115.

Kraak, W. K., Rinkel, G. L., en J. Hoogerheide, 1940. Oecologische bewerking van de Europese ringgegevens van le Kievit (*Vanellus vanellus* (L.)); Ardea 29: 151–175.

— 1942. Zwischenzug; ibid. 31: 300–302.

Krätzig, H., 1943. Beiträge zur Vogelkunde der Krim; J. Orn. 91: 268–285.

Kramer, G., 1948. Neue Beiträge zur Frage der Fernorientierung der Vögel (Ein kritischer Bericht, insbesondere über die Versuche von H. L. Yeagley); Orn. Ber.: 228–238.

— 1949. Über Richtungstendenzen bei der nächtlichen Zugunruhe gekäfigter Vögel; Ornithologie als Biologische Wissenschaft (Stresemann-Festschrift): 269–283.

— 1950. Orientierte Zugaktivität gekäfigter Singvögel; Die Naturwissenschaften 8: 188.

Krampitz, H., 1941. Erster Brutnachweis von *Larus c. canus* L. für Schlesien; Ber. Ver. Schles. Orn. 26: 49.

Kullenberg, B., 1946. Über Verbreitung und Wanderungen von vier Sterna-Arten; Ark. Zool. 38 A: 80.

Lack, D., 1943–1944. The problem of partial migration; Brit. Birds 37, 1943: 122–130, 1944: 143–150.

Lack, D., and Elisabeth Lack, 1949. Passerine migration through England; ibid. 42: 320–325.

Lack, D., and R. M. Lockley, 1938. Skokholm Bird Observatory Homing Experiments I. 1936–37. Puffins, Storm-Petrels and Manx Shearwaters; ibid. 31: 242–248.

Lack, D., and G. C. Varley, 1945. Detection Birds by radar; Nature 156: 446.

Landsberg, H., 1948. Bird Migration and Pressure Patterns; Science 108: 708–709.

Lewis, H. F., 1939. Reverse Migration; Auk 56: 13–27.

Libbert, W., 1948. Zum Herbstdurchzug des Kranichs (*G. grus*) in Nordafrika; Vogelwarte: 36–37.

Lincoln, F. C. The Migration of American Birds; New York, Doubleday, Doran & Co., New York XII: 189.

— — 1939. The Individual vs. the Species in Migration Studies; Auk 56: 250–254.

— — 1942. La Migracion de Aves en el Hemisfero Occidental; Int. Comm. Bird. Pres. New York: 12.

— — 1944. Chimney Swift's Winter Home Discovered; Auk 61: 604–609.

Lockley, 1939. Further Homing Experiment with Manx Shearwaters in 1939. My Island and Our Life There; The Countryman 20: 129–135.

Lotze, R., 1940. Das Heimfinden der Tiere; Aus d. Heimat 53: 65–75.

Lowery, G. H., 1946. Evidence of Trans-Gulf Migration; Auk 63: 175–211.

Mackintosh, D. R., 1949. The Use of Thermal Currents by Birds on Migration; Ibis 91: 55–59.

Makkink, G. F., 1946. Omgekeerde gierzwaluwentrek; Ardea 34: 264–267.

Mayaud, N., 1946. La Migration du Gobe-mouche noir, *Muscicapa hypoleuca* (Pallas) en France; Alauda 14: 44–62.

Mayr, E., 1941. Wanderung oder Ausbreitung?; Zoogeogr. 4: 18–20.

McAtee, W. L., Burleigh, T. O., Lowery, G. H., Stoddard, Fr., and H. L. Stoddard, 1944. Eastward Migration through the Gulf States; Wils. Bull. 56: 152–160.

— — 1947. Torpidity in Birds; The American Midland Naturalist 38: 191–206.

McCabe, R. A., 1947. The Homing of Transplanted Young Wood Ducks; Wils. Bull. 59: 104–109.

McIlhenny, E. A., 1940. Sex Ratio in wild Birds; Auk 57: 85–93.

McKay, H. A. C., 1945. Detection of Birds by radar; Nature: 629.

Mennig, S., 1940. A propos de l'engourdissements des Hirondelles; Gerfaut 29: 107.

Merkel, F. W., 1938. Zur Physiologie der Zugunruhe bei Vögeln; Ber. Ver. Schles. Orn. 23: 72.

— — 1939. Beobachtungen über das Zugverhalten des Rotkehlchens; ibid. 24: 63–66.

Miller, L., 1941. The directive sense in migrant Birds; Condor 43: 196.

Miller, A. H., 1948. The refractory period in light-induced reproductive development of golden-crowned sparrows; J. exp. Zool. 109: 1–11.

Moreau, R. E., 1938. Bird-Migration over the north-western Part of the Indian Ocean, the Red Sea and the Mediterranean; Proc. Zool. Soc. London, Ser. A, 108: 1–26.

Müthel, H., 1938. Hohe Zuggeschwindigkeit eines Blässhuhns, *Fulica atra;* Vogelzug 9: 206.

Neuhaus, W., 1948. Untersuchungen über die Richtungsorientierung bei Mäusen; Z. Tierpsychol. 6: 236–260.

Nice, M. M., 1946. Weights of Resident and Winter Visitant Song Sparrows in Central Ohio; Condor 48: 41–42.

Notini, G., 1947. Vingmärkning-försök med en ny märkningsmetod; Vår Fågelvärld 6: 28–37.

Öhrn, B., 1946. Ett relikt flyttningssträk av arktiska vadare över Vättern; ibid. 5: 25–28.

Oordt, G. J. van, 1940. Het Oriëntatievermogen van den Trekvogel; Voordracht gehonden: 84.

— — 1943. Vogeltrek; Leiden: 145.

OORDT, G. J. VAN, 1950. Is de Pestvogel (*Bombycilla garrulus*) een echte trekvogel?; Ardea 37: 179–181.

OTTOW, J., 1949. Ein Beitrag zur Vogelwelt des Petsamogebietes und seiner Grenzgebiete; Orn. Fenn. 26: 98–116.

PACKARD, F. M., 1946. Midsummer Wandering of Certain Rocky Mountain Birds; Auk 63: 152–158.

— — 1947. The Return of Young Robins to their Birthplaces; Bird-Band. 18: 30–31.

PAIGE, S., 1948. On Continental Drift and Bird Migration; Science 108: 711.

PALMGREN, P., 1938. Studien über den zeitlichen Ablauf der Zugerregung bei gekäfigten Kleinvögeln I; Orn. Fenn. 15: 1–16.

— 1938. Einige Labyrinthversuche mit Kleinvögeln und Mäusen; ibid. 15: 74–77.

— 1938. Zur Kausalanalyse der ökologischen und geographischen Verbreitung der Vögel Nordeuropas; Arch. Naturg. N. F. 7: 235–269.

PALMGREN, P., und Mitarbeiter, 1939. Beobachtungen über die Zugverhältnisse bei einem Wetterfrontdurchgang in Südfinnland; Vogelzug 10: 154–169.

PALMGREN, P., 1943. Eine Anlage für Registrierung der Tagesrhythmik bei Käfigvögeln; ibid. 14: 12–18.

— 1943. Zur Tagesrhythmik der Finkenvögel; Orn. Fenn. 20: 99–103.

— 1944. Tagesrhythmik gekäfigter Kleinvögel bei konstanter Dauerbeleuchtung; ibid. 21: 25–30.

— 1944. Studien über die Tagesrhythmik gekäfigter Zugvögel; Z. Tierpsychol. 6: 44–86.

1949. On the diurnal rhythm of activity and rest in birds; Ibis 91: 561–576.

PLATT, C. S., and R. S. DARE, 1945. The Homing Instinct in Pigeons; Science 101: 439–440.

PUMPHEY, R. J., 1948. The sense organs of birds; Ibis 90: 171–199.

PUTKONEN, T. A., 1942. (Zum Frühlingszug über die Bucht von Viipuri (Wiborg); Orn. Fenn. 19: 33–44. (Finnisch mit deutscher Zusammenfassung).

PUTZIG, P., 1938. Über das Zugverhalten umgesiedelter englischer Stockenten (*Anas p. platyrhyncha*); Vogelzug 9: 139–145.

1938. Weitere Versuche über die Beziehungen der Keimdrüsen zum Zugverhalten; ibid. 9: 189–200.

— 1938. Die Wanderungen des Eichelhähers (*Garrulus glandarius* L.) im Lichte neuerer Ergebnisse; Schr. Phys.-ökon. Ges. Königsberg 70: 189–216.

— 1938. Die Triebkräfte des Vogelzuges; Umschau 42: 866–869.

— 1938. Versuche über das Zugverhalten von Stockenten; Wild und Hund 44: 795.

— 1939. Keimdrüsen und Heimzug; Ber. Ver. Schles. Orn. 24: 36–41.

— 1939. Beiträge zur Stoffwechselphysiologie des Zugvogels; Vogelzug 10: 139–154.

1939. Sechste Rückmeldung einer kastrierten Nebelkrähe (*Corvus cornix*) in Heimzugrichtung; ibid. 10: 171–172.

— — 1939. Problematik und Stand der Vogelzugforschung; Gef. Welt 68: 458, 468, 478, 489, 498, 505.

RENSE, W. A., 1946. Astronomy and Ornithology; Popular Astronomy 54: 1–19.

RITCHIE, J., 1940. An analysis of the influence of weather upon a migratory movement of birds; Proc. Roy. Soc. Edinb. 60: 299–321.

ROBERTS, B., 1940. The life cycle of Wilson's Petrel, *Oceanites oceanicus* (Kuhl); Sci. Rep. Brit. Graham Land Exped. 1934–37 (London) 1: 141–194.

ROLLO, MARIE, 1941. Photoperiodism and Migration; Bird-Band. 12: 161–164.

ROOMWAL, M. L., 1940. Migration of Birds; Sci. and Culture Calcutta 5: 669–678.

ROWAN, W., 1945. Homing, Migration and Instinct; Science 102: 210–211.

Rowan, W., 1946. Experiments in Bird Migration; Transact. Royal. Soc. Canada 3. Ser. Sect. V, 40: 123–135.

Rowan, W., and A. M. Batrawi, 1939. Comments on the Gonads of some European Migrants collected in East Africa immediately before their Spring Departure; Ibis 14. Ser. 3: 58–65.

Rudebeck, G., och G. Svärdson, 1946. En rubbning i flyttfågelsträcket våren 1944; Vår Fågelvärld 5: 16–25.

Rüppell, W., 1940. Neue Ergebnisse über das Heimfinden beim Habicht; Vogelzug 11: 57–64.

— — 1944. Versuche über Heimfinden ziehender Nebelkrähen nach Verfrachtung; J. Orn. 92: 106–132.

— — 1948. Heimkehr verfrachteter Habichte (*Accipiter gentilis*) aus 300 und 600 km Entfernung; Vogelwarte 15, 1: 39.

Rüppell, W., und W. Schein, 1941. Über das Heimfinden freilebender Stare bei Verfrachtung nach einjähriger Freiheitsentziehung am Heimatort; Vogelzug 12: 49–56.

Rüppell, W., und A. Schifferli, 1939. Versuche über Winter-Ortstreue an *Larus ridibundus* und *Fulica atra* 1935; J. Orn. 87: 224–239.

Rüppell, W., und E. Schüz, 1948. Ergebnis der Verfrachtung von Nebelkrähen (*Corvus corone cornix*) während des Wegzuges; Vogelwarte 15, 1: 30–36.

Rust, H. J., 1947. Migration and nesting of Nighthawks in Northern Idaho; Condor 49: 177–188.

Salomonsen, F., 1949. Nye teorier om trækfuglenes orientering; Dansk. Orn. For. Tidskr. 43: 242–250.

Salomonsen, E., 1938. Fugletrækket over Danmark; Kopenhagen: 228.

Savile, D. B. O., 1948. Bird Navigation in Homing and in Migration; Science 107: 596–597.

Schifferli, A., 1943. Nachtrag zu Transportversuchen mit Futterplatzvögeln im Herbst und Winter; Orn. Beob. 40: 43.

— — 1943. Brandente (*Tadorna tadorna*) kehrt nach Sempach zurück; ibid. 40: 44.

Schildmacher, H., 1938. Zur Physiologie des Zugtriebes IV. Weitere Versuche mit künstlich veränderter Belichtungszeit; Vogelzug 9: 146–152.

— — 1938. Hoden und Schilddrüsen des Gartenrotschwanzes, *Phoenicurus ph. phoenicurus* (L.) unter den Einfluss zusätzlicher Belichtung; Biol. Zbl. 58: 464–472.

— — 1939. Über die künstliche Aktivierung der Hoden einiger Vogelarten im Herbst durch Belichtung und Vorderlappenhormone; ibid. 59: 653–657.

Schumacher, W. C., 1949. "A Preliminary Study of a Physical Basis of Bird Migration"; J. appl. Phys. 20.

Schuster, L., 1940. Langjährige Wiederkehr eines Mäusebussards (*Buteo buteo*) an denselben Überwinterungsplatz; Vogelzug 11: 86.

Schüz, E., 1942. Die Geschichte einer Lachmöwe; Deutsche Vogelwelt 67: 6–9.

— — 1941–1945. Der europäische Rauhfussbussard, *Buteo l. lagopus* (Brünn.) als Invasionsvogel; Jahresh. Verh. Vaterl. Naturk. Württemberg 97–101: 125–150.

— — 1949. Die Spät-Auflassung ostpreussischer Jungstörche in Westdeutschland durch die Vogelwarte Rossitten 1933; Vogelwarte: 63–78.

Severn Wildfowl Trust, 1948. Annual Report 1948. London: 72.

Shaw, Tsen-Hwang, 1939. Variability in the body weight of the Brambling; Bull. Fan. Mem. Inst. Biol., Zool. Ser. 9: 241–250.

Siivonen, L., 1941. Über die Kausalzusammenhänge der Wanderungen beim Seidenschwanz, *Bombycilla g. garrulus* (L.); Ann. Soc. zool.-bot. Fenn. 8: 40.

Sinding, E., 1947. Bestemmelse af Fugletrækkets Høde ved Hjælp af Afstandsmaaler; Dansk. Orn. For. Tidskr. 41: 56–60.

Slepian, J., 1948. Physical Basis of Bird Navigation; J. appl. Physics, 19: 306.

SLIVINSKY, URSULA, 1938. Isopiptesen einiger Vogelarten in Europa; Zool. Poloniae 2: 249–287.

SOUTHERN, N. H., 1938. The Spring Migration of the Swallow over Europe; Brit. Birds 32: 4–7.

— — 1938. The Spring Migration of the Willow-Warbler over Europe; ibid. 32: 202–206.

— — 1939. The Spring Migration of the Redstart over Europe; ibid. 33: 34–38.

— — 1940. The Spring Migration of the Wood-Warbler over Europe; ibid. 34: 74–79.

— — 1941. The Spring Migration of the Red-Backed Shrike over Europe; ibid. 35: 114–119.

STADIE, R., 1938. Experimentelle Untersuchungen über den Wandertrieb gekäfigter Gartenrotschwänze, *Phoenicurus ph. phoenicurus* (L.); Ber. Ver. Schles. Orn. 23: 65–80.

(— —) 1938. Sturmöwen der pommerschen Ostseeküste im Binnenland; Wild und Hund 44: 701.

STEINBACHER, J., 1939: Singen unsere Vögel im Winterquartier?; Gef. Welt 68: 341–343.

STIMMELMAYR, A., 1942. Das grosse Geheimnis von Raum und Zeit im Leben der Natur; Landshut-Bayern: 62.

STRAUTZELS, T., 1938. (Verlauf des Anflugs einiger Zugvögel Lettlands); Riga: 16 (lettisch mit deutscher Zusammenfassung).

STRESEMANN, E., 1940. Zeitpunkt und Verlauf der Mauser bei einigen Entenarten; J. Orn. 88: 288–333.

— — 1944. Der zeitliche Ablauf des Frühjahrszuges beim Neuntöter (*Lanius collurio*); Orn. Mber. 52: 1–8.

— — 1944. Der Frühjahrsdurchzug einiger Vogelarten durch die Mittelmeerländer; ibid. 52: 29–44.

— — 1944. Der zeitliche Ablauf des Frühjahrszuges beim Kappenammer, *Emberiza melanocephala* Scop.; ibid. 52: 85–92.

— — 1944. Die Sahara als Durchzugsgebiet europäischer Vögel; ibid. 52: 126–132.

— — 1947. Der zeitliche Ablauf des Frühjahrszuges bei Nachtigall und Sprosser; Orn. Ber.: 1–10.

— — 1948. Die Wanderungen des Pirols (*Oriolus o. oriolus*); ibid.: 126–142.

— — 1948. Die mittlere Erstankunft von *Lanius collurio*, *Muscicapa striata*, *Oriolus oriolus* und *Oenanthe oenanthe* im europäischen Brutraum; Vår Fågelvärld 7: 1–18.

SVÄRDSON, G., 1948–1950. Verksamheten vid Ottenby fågelstation; Vår Fågelvärld: 7–9.

— — 1949. Skruvflykt hos flyttande måsar; ibid. 8: 13–33.

SWANBERG, P. O., 1948. Ett tillfälligt återsträck av bofinkar den 3 april 1947; ibid. 7: 125–126, 128.

TETTENBORN, W., 1943. Feststellungen an beringten Lachmöwen in Berlin, Winter 1942/43; J. Orn. 91: 286–295.

THOMSON, A. L., 1945. Bird migration; a short account. Revised ed. London: 192.

THOMSON, A. L., and D. H. WILKINSON, 1946. Ising's theory of bird orientation; Nature London 158: 903–904.

THORPE, W. H., 1949. Recent Biological Evidence for the Methods of Bird Orientation: Proc. Linn. Soc. London 160: 85–94.

TINBERGEN, L., 1941. Over de Trekwegen van Vinken (*Fringilla coelebs* L.); Ardea 30: 42–73.

— — 1941. Over de rol van de Hollandse duinrij by de oriëntatie von trekkende vinken en spreeuwen; Limosa 14: 1–20.

— — 1942. De dagtrek in de herfst van 1940 over westelijk Zuid-Holland; Ardea 31: 153–154.

— — 1949. Vogels onderweg. Vogeltrek over Nederland in samenhang met landschap, weer en wind; Amsterdam: 110.

TOSCHI, A., 1939. La Migrazione degli Uccelli; Supplem. Ric. Zool. appl. a Caccia, Bologna: 292.

TUGARINOW, A. J., 1949. Der heutige Stand der Vogelzugsforschung; Mitt. Akad. d. Wissenschaften, Biolog. Serie 1: 7–29 (russisch).

VÄLIKANGAS, J., 1946. J. A. Palméns Theories on migratory routes of birds in the light of later,

especially Finnish, Observations and results of ring-marking; Soc. sc. fenn. Årsbok-Vuosikirja 24: 34.

Varian, R. H., 1948. Remarks on: "A Preliminary Study of a Physical Basis of Bird Migration"; J. appl. Phys. 19: 306–307.

Verheyen, D. R., 1947. Un aperçu général du problème de la migration des oiseaux; Gerfaut 37: 1–14.

Verwey, J., 1949. Migration in Birds and Fishes; Bijdragen tot de Dierkunde 28: 477–503.

Vleugel, D. A., 1943. Waarnemingen betreffende den Vorjaarstrek van den Vink (*Fringilla coelebs* L.) bij Nijmwegen; Ardea 32: 250-263.

—— 1948. Enkele waarnemingen over "vorstvlucht" en "randtrek" in het Sloe-Schengengebied tijdens de winters van 1935/1936 en 1936/1937; ibid. 36: 143-162.

Wagner, H. O., 1941. Der Durchzug von *Buteo swainsoni* in Centralamerika; Orn. Mber. 49: 162–166.

Wallace, G. J., 1941. Winter Studies of Color-Banded Chikadees; Bird-Band. 12: 49-67.

Warga, K., 1935–1938. Die *Bombycilla g. garrulus* Invasion in den Jahren 1931/32 und 1932/33 und die Ergebnisse der Beringungsversuche; Aquila 42/45: 410–542.

Waterhouse, M. J., 1949. Rook and Jackdaw Migrations Observed in Germany, 1942–1945; Ibis 91: 1–16.

Watson, J., 1945. The migration of birds-facts and fancies; Vict. Nat. Melbourne 62: 20–26.

Werner, Cl. F., 1939. Die Otolithen im Labyrinth der Vögel, besonders beim Star und der Taube; J. Orn. 87: 10–23.

Wilkinson, D. H., 1949. Some physical Principles of Bird Orientation; Proc. Linn. Soc. London 160: 94-99.

Willett, G., 1946. Migration of North American Birds; Quart. Los Angeles County Mus. 5: 3–13.

Williams, G. G., 1950. Weather and Spring Migration; Auk 67: 52–65.

Wing, L., 1941. Size of Bird Flocks in Winter; ibid. 58: 188–194.

Wodzicki, Graf K., Puchalski, W., und H. Liche, 1939. Untersuchungen über Orientierung und Geschwindigkeit des Fluges bei Vögeln V. Weitere Versuche an Störchen; J. Orn. 87: 99-114.

Wojtusiak, R. J., 1949. Polish Investigations on Homing in Birds and their Orientation in Space; Proc. Linn. Soc. London 160: 99–108.

Wojtusiak, R. J., und B. Ferens, 1938. Untersuchungen über die Orientation und Geschwindigkeit des Fluges bei Vögeln IV. Heimkehrgeschwindigkeit und Orientierungsart bei den Rauchschwalben (*Hirundo rustica* L.); Bull. de l'Akad. Polon. d. Sc. et d. Lettres, Krakau: 173–201.

Wolfson, A., 1940. A preliminary report on some experiments on bird migration; Condor 42: 93-99.

—— 1941. Light versus activity in the regulation of the sexual cycles of birds: the role of the hypothalamus; ibid. 43: 125-136.

—— 1942. Regulation of spring migration in Juncos; ibid. 44: 237–263.

—— 1945. The role of the pituitary, fat deposition, and body weight in bird migration; ibid. 47: 95–127.

—— 1948. Bird Migration and the Concept of Continental Drift; Science 108: 23–30.

Woodbury, A. M., 1941. Animal migration — Periodic-response theory; Auk 58: 463-505.

Woodcock, A. H., 1940. Herring gull soaring; ibid. 57: 219-224.

Wynne-Edwards, V. C., 1948. Yeagley's Theory of Bird Navigation; Ibis 90: 606–611.

Yeagley, H. L., 1947. A preliminary study of a physical basis of bird navigation; J. appl. Physics 18: 1035–1063.

# Reproduction, Migration and Moult: Factors Controlling the Annual Cycle in Birds

*A. Landsborough Thomson*

*London*

Recent papers by Lack (1950 a, 1950 b), Moreau (1950 a, 1950 b), Skutch (1950), and Voous (1950) have added substantially to understanding of the factors which determine the time of the breeding season in different species of birds in various parts of the world. In an introductory review of these papers, the present writer (Thomson, 1950) briefly drew a parallel with the timing of migration. The purpose of this note is to elaborate that point, taking an integrated view of the whole annual cycle of the bird's life.

In the great majority of cases, the cycle is in fact an annual one. This is obvious and invariable in the higher latitudes, where the seasons are strongly contrasted. To a very considerable extent an annual periodicity is apparent also in the tropics.

The question is how the bird's annual cycle is related to the annual cycle of the environment. This has two aspects. Firstly, it is clear that the events in the bird's year must be adapted to the changes in the environment, as a result of natural selection. Secondly, there must be a timing operation bringing this adaptation punctually into play. The distinction is fundamental.

Migration, except in the case of "weather movements" and the like, is not stimulated by the actual conditions to which it is primarily adapted. Migration from the breeding area is adapted to secure avoidance of the conditions of winter, but it may begin in autumn or even late summer before the impact of these conditions can be felt. Migration to the breeding area is adapted to secure the exploitation of the opportunities for reproduction which that area provides, but it begins in another area where quite different conditions may prevail. The writer (Thomson, 1926, 1936) has discussed these points more fully elsewhere.

Similarly, with regard to reproduction, the recent work has clearly brought out that the time of breeding is commonly adapted to secure that the maximum supply of appropriate food will be available when the young are hatched and for a sufficient time after they are first on the wing. That is to say, the beginning of the breeding season is timed in adaptation to environmental conditions which do not operate until towards its close. It is true that suitable conditions for nesting must be available at the beginning of the breeding season, and sometimes this is crucial; but as a general rule, within the limits of the possible, nesting convenience seems to be subordinated to the later requirement of food for the young.

Moulting is in the main interpolated between the breeding season and the times of migration, where the latter occurs; and this applies whether there are two moults in the year or only one. Obviously, the stress and partial incapacity involved would be incompatible with the intense activity of the breeding season. Equally, migration would be impracticable during the moult of the quill feathers, although some species may show moult of the smaller body feathers during migration. Most passerine birds have their autumn moult between the end of the breeding season and the beginning of migration; in some other migratory birds moulting does not take place until the winter-quarters are reached. Where there is a spring moult, it normally precedes migration and reproduction. One may therefore regard the timing of the moult as a secondary adaptation, which in the main keeps moulting clear of the periods of reproduction and migration.

It is evident that reproduction and migration are both timed in adaptation to factors which operate at their end rather than at their beginning: these are "ultimate" factors. The new evidence emphasises the importance of food-supply, particularly for the young birds, as the environmental factor to which the time of the breeding season is commonly adapted. The timing of migration may be regarded as secondary to the timing of the over-riding requirement of reproduction. Furthermore, it has for long been considered that food-supply is the chief factor to which migration is itself adapted; that scarcity of food, coupled in some cases with shorter hours of daylight and harder conditions for obtaining it, is a more serious rigour of winter than the direct effects of cold and storm; and that abundant food-supply is one of the main opportunities to be exploited in the breeding area. So one may conclude that the timing of the whole annual cycle is largely an adaptation to conditions of food-supply.

On the other hand the several events occur before the conditions to which each is adapted are in actual operation. There must therefore also be "proximate" factors which act as stimuli to the inception of the various activities. These may be sought in changes in the environment occurring at the appropriate times of year. In higher latitudes, those which suggest themselves are changes in temperature and changes in length of day. The work of Rowan (1926, 1929), and of Bissonnette (1930, etc.) and others, has provided evidence of the operation of the latter; and recent evidence of the effect of temperature on the beginning of reproduction is that given by Marshall (1949). In the tropics, the chief change in the environment is commonly in humidity and rainfall. Lack (1950 a) has cited evidence that rain may be a stimulus to reproduction in the case of the Galapagos finches; on the other hand, in some tropical areas breeding begins well in advance of the first rainfall.

The proximate factor cannot be the same in all cases. The extrinsic stimulus which operates in inducing reproduction or migration must be different in higher latitudes from what it is in the tropics; and, in the case of a bird which migrates from a temperate area to the tropics, the stimulus to migration must be different in kind in autumn and in the time of year corresponding with spring. There is the additional point that separate communities of a species, subject at a particular time to the same extrinsic stimuli, may react differently; examples have been given by Bullough (1942) and Blanchard (1942) in respect of the native and winter visitant members of a species in a given area.

There is the further possibility that the annual cycle of the bird's life is linked at only one point with environmental stimuli; that an inherent rhythm has been established; and that all but one of the events in the cycle occur as the result of the mere effluxion of time, following refractory periods—to the importance of which Burger (1949) has recently drawn attention. This would serve to explain the migration of a bird, native to temperate latitudes, from a part of the tropics in which environmental conditions are highly constant. There is evidence for it in the fact that some species, when artificially transported from the southern to the northern hemisphere, do not readily adapt their breeding times to the reversal of the climatic seasons. It also seems possible that the stimulus to moulting is of this kind.

It is not within the scope of the present contribution to discuss the physiological mechanism through which the various stimuli may act. One may nevertheless note the suggestion of Wolfson (1940) that "the total physiological and psychological state of the bird is important in inducing migratory and breeding behaviour and not the physiological condition of one organ alone."

## Conclusion

From all these considerations there emerges the general conception of an annual physiological cycle, established to a greater or less extent as an inherent rhythm, linked proximately to one or more environmental factors of various kinds which control the timing, and adapted ultimately to conditions of the environment of which food-supply is the most important.

## References

Bissonnette, T. H., 1930. Studies on the sexual cycle in birds. — 1. Sexual maturity, its modification and possible control in the European Starling (*Sturnus vulgaris*). Amer. J. Anat., 45: 289—305.

Blanchard, B. D., 1942. Migration in Pacific Coast White-Crowned Sparrows. Auk, 59: 47–63.

Bullogh, W. S., 1942. The reproductive cycles of the British and Continental races of the Starling. Phil. Trans. R. Soc. London (B), 231: 165–246.

Burger, J. W., 1949. A review of experimental investigations of seasonal reproduction in birds. Wilson Bull., 61: 211–230.

Lack, D., 1950 a. Breeding seasons in the Galapagos. Ibis, 92: 268–278.

—— 1950 b. The breeding seasons of European birds. Ibis, 92: 288–316.

Marshall, A. J., 1949. Weather factors and spermatogenesis in birds. Proc. Zool. Soc. London, 119: 711-716.

Moreau, R. E., 1950 a. The breeding seasons of African birds. — 1. Land-birds. Ibis, 92: 223-267.

—— 1950 b. The breeding seasons of African birds. — 2. Sea-birds. Ibis, 92: 419–433.

Rowan, W., 1926. On photoperiodism, reproductive periodicity and the annual migrations of certain birds and fishes. Proc. Boston Soc. Nat. Hist., 38: 147–189.

—— 1929. Experiments in bird-migration. — 1. Manipulation of the reproductive cycle: seasonal changes in the gonads. Proc. Boston Soc. Nat. Hist., 39: 151–208.

Skutch, A. F., 1950. The nesting seasons of Central American birds in relation to climate and food supply. Ibis, 92: 185–222.

Thomson, A. L., 1926. Problems of Bird Migration, London and Boston.

—— 1936. Recent progress in the study of bird-migration: a review of the literature, 1926–35. Ibis, (13) 6: 472-530.

—— 1950. Factors determining the breeding seasons of birds: an introductory review. Ibis, 92: 173–184.

Voous, K. H., 1950. The breeding seasons of birds in Indonesia. Ibis, 92: 279–287.

Wolfson, A., 1940. A preliminary report on some experiments on bird-migration. Condor, 42: 93–99.

# The Migration System in Perspective

*R. E. Moreau*

*Edward Grey Institute, Department of Zoological Field Studies, Oxford*

Since most ornithologists live in the North Temperate Zone it is inevitable that discussion of migration should have been dominated by the very impressive phenomena that we observe here. Also it is understandable that, in considering the problem of the origin of migration, the great climatic changes at high latitudes involved in the glaciations of the Pleistocene should have been regarded as of prime importance.

Twenty years ago Mayr and Meise (1930) applied a corrective to these relatively short and limited views of migration. They regarded migration as having originated in localities where, owing to seasonal changes in climate, fewer birds could find food at one time of the year than at another. If they moved away at a time of scarcity, some birds might have a better chance of survival than others, and hence natural selection would develop migration. It follows that the origin of migration could be much older than the Pleistocene glaciations and need have nothing to do with an inherited longing for an area from which a bird's ancestors had been driven by advancing ice.

With these views I emphatically agree; and in my opinion they can be supported by a number of different considerations. In the first place, the spectacular climatic fluctuations of the Pleistocene all occurred during less than the last one million years, a period less than one hundredth part of the age of the class Aves. But already by the Eocene the main families of birds are identifiable in the fossil record, and by the Oligocene actually some of the existing genera, which today provide thoroughly characteristic migrants, for example, *Puffinus, Tringa, Motacilla* and *Lanius* (Howard, 1950). Thus, it is clear that birds capable of long-distance migration existed over thirty times as long ago as the first of the Pleistocene glaciations.

The term "migrant" of course includes birds of a great variety of achievement. Some, like *Hirundo rustica* and *Sterna macrura,* regularly travel

10 000 km; and there is every gradation in length of journey, down to those of a few kilometers, from mountain to plain, which are better classified as change of habitat. But for the present discussion I shall regard as typical long-distance migrants those species which make journeys of at least 1 000 km—like, for example, *Turdus pilaris* coming from Scandinavia to winter in England. It is instructive to see how migrations comparable to this can be quoted from other parts of the world which were far outside the range of the Pleistocene ice-cap.

Taking first the sub-tropics, we have great autumnal movements from the Mediterranean Basin, including French North Africa and even the more or less evergreen irrigated Delta of Egypt. From there several species fly south for more than 1 500 km. The Saharan desert belt is so severe and so wide that it would be of no use for these birds to travel any lesser distance; but at the southern end of the African continent, again around 30° from the equator, where there is no such overwhelmingly important desert belt, a number of birds migrate for an equally long distance, for example swallows (*H. albigularis* and *H. cucullata*) and the various cuckoos, from Cape Province to north of the Zambesi, at least 1 500 km.

In sub-tropical Australia, especially South Australia and New South Wales, many species are breeding migrants (cf. Chisholm 1934) and New Zealand provides three examples of remarkably long migration. *Charadrius bicinctus* crosses 2 000 km of sea to Australia, *Chalcites lucidus* and *Eudynamis taitensis* even more sea, to New Caledonia, the Solomons and Polynesia.

In America Wetmore (1926) has drawn attention to the fact that in Paraguay and in Argentina round about 32° S. "migratory movements are as readily evident to the field observer as in northern regions". North of the equator the Florida population of *Haliaeetus l. leucocephalus* performs a remarkable migration, for after breeding in Florida in mid-winter it actually flies north as far as eastern Canada, 1 500 km away (Broley, 1947).

Finally, in the sub-tropics we may cite the five species of *Puffinus*, including the familiar *P. gravis* of the Tristan da Cunha group, which breed at about 35° S. and travel 7 000 km or more northwards to winter.

The actual tropical belt of the world is by no means all favourable to bird-life all the year round. Even on the equator itself one finds in Africa, besides evergreen conditions, also a regime with two rainy and two dry seasons, and also what is nearly desert. As one would expect therefore, there is much seasonal movement among those very numerous tropical birds which do not inhabit evergreen forest. Several species that breed on the southern edge of the Sahara in the rains thereafter cross into the southern tropics for their off-season and have a displacement of on the average at least 1500 km. *Sphenorynchus* (Ciconiidae) moves south from the Sudan for an even longer distance, and *Cosmetornis* (Caprimulgidae) performs a comparable movement in the opposite direction, after breeding in the south.

At least some of the African migrants travel by night, just like long-distance Palaearctic migrants. I had personal experience of this when I was living at Amani, at 5° S., where *Pitta angolensis* and *Coturnix delegorguei*, for example, often came to lighted windows.

In tropical Australia several species arrive annually from across the seas to the north, some from as far as the Bismarcks and the Solomons (Mayr, 1945). Eastern Asia has a remarkable case in *Eurystomus orientalis deignani*, travelling from northern Siam as far as Borneo and Java (Peters, 1945), another flight of 3 000 km wholly within the tropics. This is equalled by another roller, *Eurystomus glaucurus*, of Madagascar, which "winters" as far away as the northern Belgian Congo (Chapin, 1932), and also by the Indian population of the cuckoo *Clamator jacobinus*, which travels all the way to East Africa after breeding. On the other side of the world, in the West Indies, as Dr. J. Bond informs me, *Tyrannus dominicensis* and *Vireo altiloquus* migrate from the Bahamas and Cuba across the Carribean Sea to Colombia.

The foregoing examples of long-distance migrations all come from low latitudes not directly affected by Pleistocene glaciations and were presumably developed independently of them. Such movements may well be far older than the Pleistocene, especially as we know that birds capable of migration already existed at the beginning of Tertiary time. It is, then, important to know what environments the world provided in these earlier epochs.

As Brooks (1949) has pointed out, there is no doubt that "the popular conception of a geological landscape" as "a steaming jungle" is wrong. Climatologists are satisfied that climatic zones on the present system must always have existed, although in the early Tertiary the coldest zones were absent and the other zones were correspondingly broader (cf. Schwarzbach, 1946). On theoretical grounds the sequence of equatorial rain-belt, monsoon belt (single, summer, rainy season), desert, Mediterranean-type belt (winter rainy season) must have existed — and fossil evidence, for example of Eocene desert in northern Africa, supports this. Most of these climatic belts undergo great seasonal changes in their vegetation and so could support far fewer birds at one season of the year than at another. Natural selection would therefore have been favourable to migration even thus early in the Tertiary, and migration must often have been long because a desert, or the Tethys Sea, had to be crossed to reach any country worth reaching.

To summarize the point of view here presented: it seems that on this perspective it is right to regard the present immense phenomena of Palaearctic and Nearctic migration as representing, on the geological time-scale, only a temporary stage of a process and a system as old as well-developed flight. The Pleistocene climatic fluctuations have done no more than determine the details of the specific migrations we see.

## References

Broley, C. L., 1947. Migration and nesting of Florida Bald Eagles. Wilson Bull. 59: 3–20.

Brooks, C. E. P., 1949. Climate through the ages. 2 ed. London.

Chapin, J. P., 1932. Birds of the Belgian Congo — 1. Bull. Amer. Mus. Nat. Hist. 65.

Chisholm, A. H., 1934. Bird wonders of Australia. Sydney.

Howard, H., 1950. Fossil evidence of avian evolution. Ibis 92: 1–21.

Mayr, E., 1945. Birds of the Southwest Pacific. New York.

Mayr, E. and Meise, W., 1930. Theoretisches zur Geschichte des Vogelzugs. Vogelzug 1: 149-172.

Peters, J. L., 1945. Check list of the birds of the world. Cambridge, Mass.

Schwarzbach, M., 1946. Klima and Klimagürtel im Alttertiär. Naturwissenschaften 33: 355–361.

Wetmore, A., 1926. Observations on the birds of Argentina, Paraguay, Uruguay and Chile. U.S. Nat. Mus. Bull. 133.

# Überblick über die Orientierungsversuche der Vogelwarte Rossitten (jetzt: Vogelwarte Radolfzell)

Ringfund-Mitteilung der Vogelwarte Radolfzell (262) und der Vogelwarte Helgoland (219)

*Ernst Schüz*

*Vogelwarte Radolfzell, Bodensee*

Die Vogelwarte Rossitten hat 1944/45 ihre alte Wirkungsstätte aufgeben müssen und arbeitet seit 1946 als „Vogelwarte Radolfzell — vormals Vogelwarte Rossitten — der Max-Planck-Gesellschaft zur Förderung der Wissenschaften“ an einem neuen Ort weiter: in Schloss Möggingen bei Radolfzell am Bodensee. Da die Vogelwarte demnächst auf eine 50jährige Tätigkeit zurückblicken kann und da der Krieg einen so tiefen Einschnitt darin bedeutet, ist es angebracht, eine Rückschau auf ein besonderes Arbeitsfeld dieser Vogelwarte zu geben, nämlich auf die Versuche zur Frage des Sichzurechtfindens der Zugvögel.

Diese Versuche, die auf Anfängen von J. Thienemann aufbauen, sind — wie fast alle Vogelwarteforschung — eine Gemeinschaftsarbeit, an der viele teilhaben; ja auch andere Vogelwarten und deren Mitarbeiterstäbe haben darin wieder mit uns zusammengewirkt, wobei besonders die Vogelwarte Helgoland und die Vogelwarte Sempach hervorzuheben sind. Rühmlich erwähnt sei unser geschätzter Mitarbeiter Werner Rüppell, der sowohl während seiner Rossittener Zeit als auch nachher immer wieder eigene Gedanken beitrug und zur Durchführung brachte. Da dies stets in enger Zusammenarbeit mit uns geschah, ist es nicht möglich, diese Rüppellschen Versuche (vgl. Versuche 3 b, 4, 5, 6) ganz abzugrenzen. So möge dieser Überblick auch sie einschliessen und damit gleichzeitig ein Erinnerungsblatt für unseren hervorragenden Mitarbeiter darstellen, dessen Tod einen so schmerzlichen Verlust auch für seine Fachfreunde bedeutet. Die vielen weiteren Mithelfer zu nennen, verbietet der Platzmangel. Ohne die tatkräftige Hilfe der Deutschen Forschungsgemeinschaft (Notgemeinschaft der Deutschen Wissenschaft) wäre mancher Versuch unmöglich gewesen.

Infolge der geforderten Beschränkung muss die geplante Kurzwiedergabe

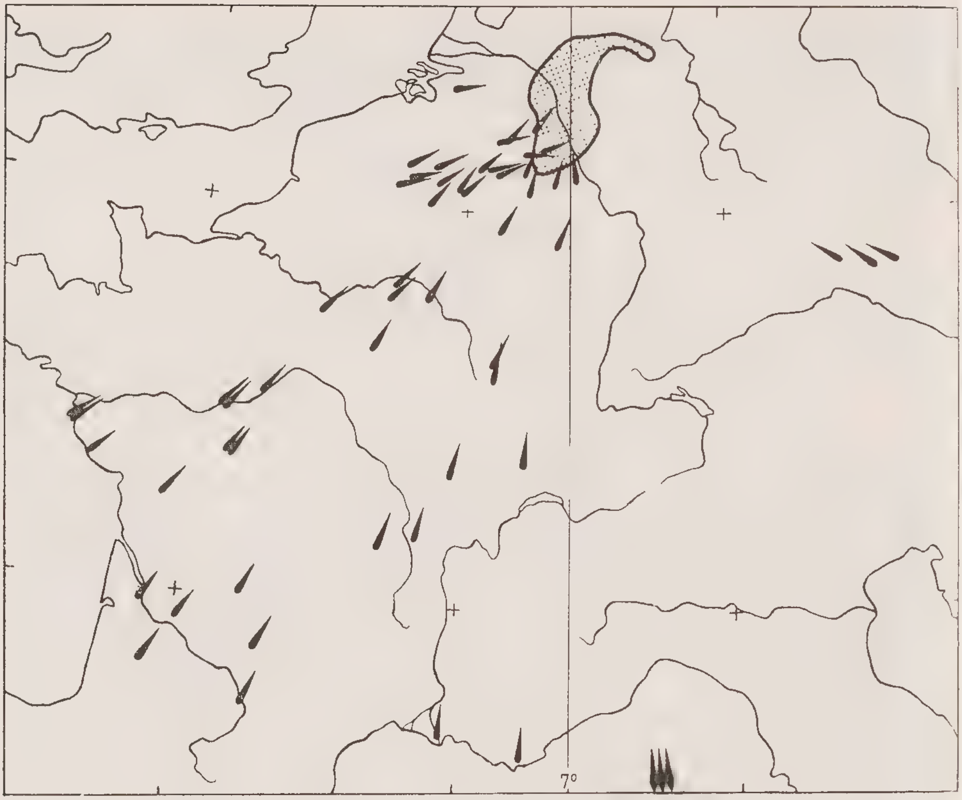


Fig. 1. In den Jahren 1933 bis 1936 wurden 754 ostpreussische Jungstörche von einzelnen Storchfreunden im Westen auf Kunsthorsten grossgezogen, im übrigen aber völliger Freiheit überlassen (Versuch 2 b). Sie ergaben mehr als 100 Wiederfunde. Die Karte beschränkt sich auf die Aufzuchten im Bereich des Niederrheins bis Westfalen (Ostpunkt Bad Salzuflen) und auf die bis 13. September des Geburtsjahres erzielten Funde, die einem ungestörten Ablauf entsprechen dürften. Von diesen Nachweisen liegen 50 im SW-Sektor (zwischen W und S, die meisten nach SW) und 7 im SE-Sektor (fast S bis ESE). Diese Anpassung an die veränderten Bedingungen geht offenkundig auf Anschluss an freilebende (durchziehende) West-Störche (vgl. Fig. 2) zurück, worüber mehrfache unmittelbare Beobachtungen vorliegen. Vgl. den ausserordentlichen Gegensatz zu Fig. 3!

des Tatbestandes der einzelnen Versuche auf eine spätere Gelegenheit verschoben werden. Wir müssen uns also mit Titelangaben und Andeutungen begnügen (I), um noch Raum für die Auswertung, wenn auch in kürzester Form, übrigzuhaben (II).

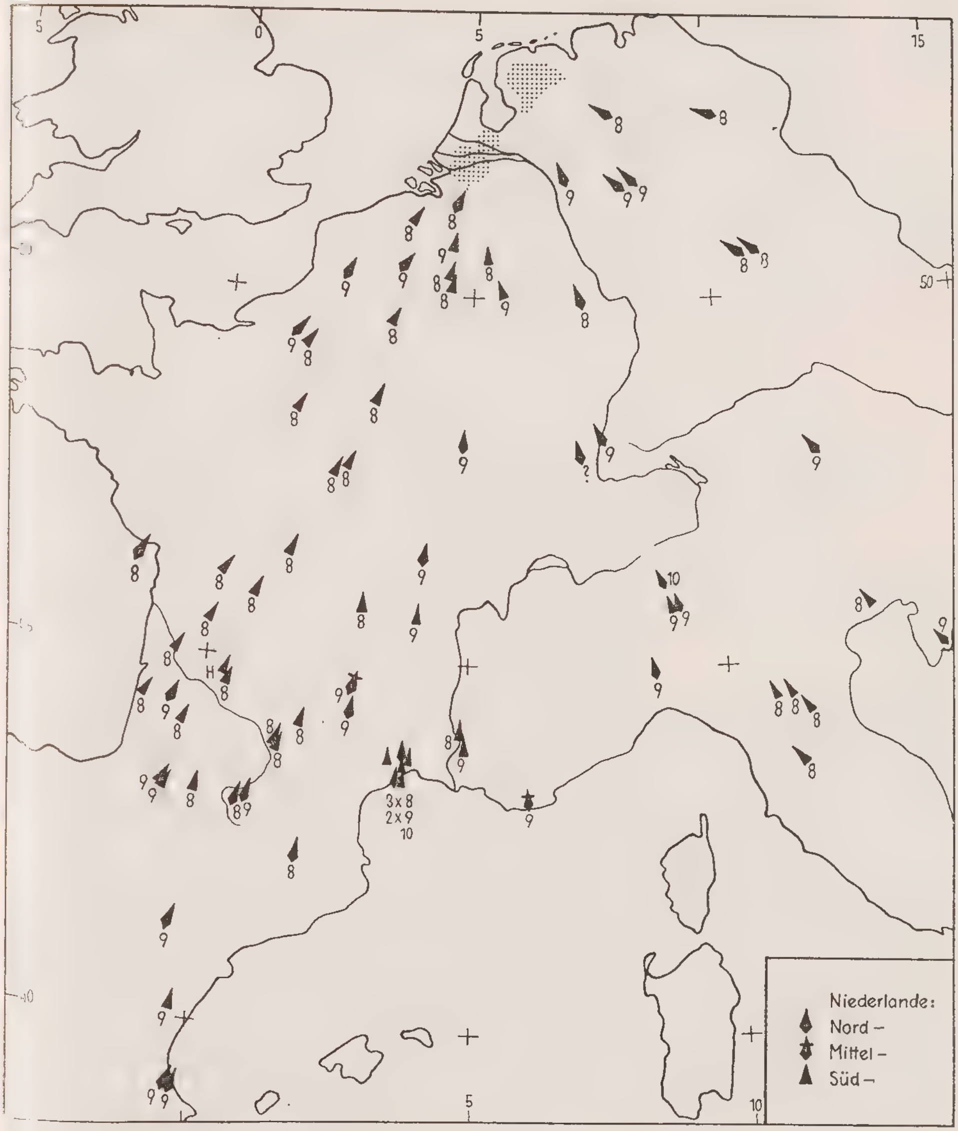


Fig. 2. Europa-Funde niederländischer Störche bis etwa 14° E, nur erster Wegzug; zusammengestellt nach den Listen der Beringungszentrale Leiden und nach F. Haverschmidt 1949. Das Verhältnis der West- zu den Ostvögeln ist auf der Karte 51 : 25, bei Einbeziehung der Europafunde jenseits Kartenrand 51 : 35. Der Grat der Zugscheide (Leiden—Giessen—Würzburg—Kempten) halbiert ungefähr das niederländische Beringungsgebiet, während das Aufzuchtgebiet der ostpreussischen Versuchsstörche nach Fig. 1 grösstenteils südwestlich dieser Linie liegt. So ist der grössere Anteil östlicher Störche bei den Niederländern verständlich, ebenso der stark gleitende Übergang zwischen W und E, verglichen mit dem Verhalten der Versuchsvögel im deutschen Niederrheingebiet.

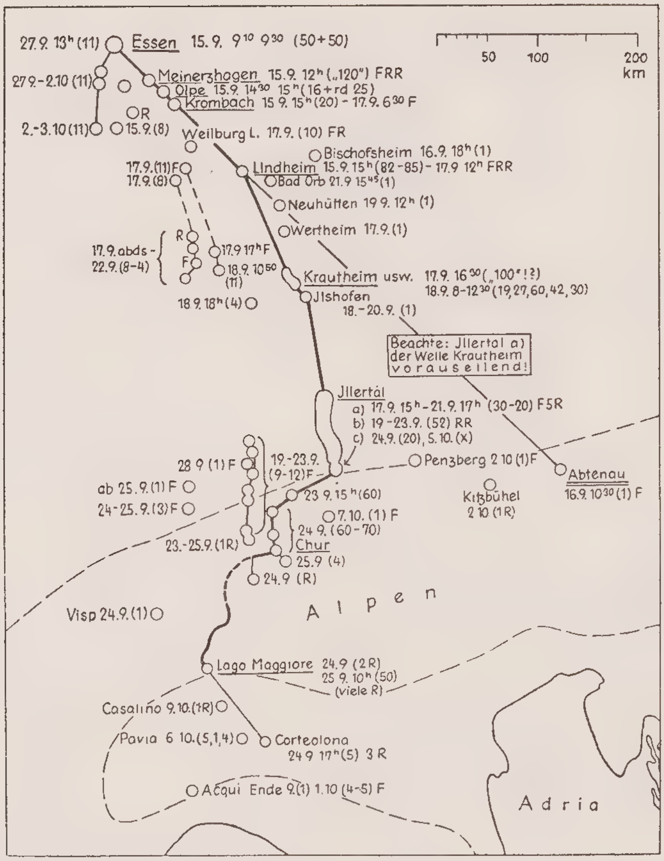

27.9. $13^h$ (11)
Essen 15.9. $9^{10}$ $9^{30}$ (50+50)
50
100
200 km
27.9.-2.10 (11)
Meinerzhagen 15.9. $12^h$ („120") FRR
Olpe 15.9. $14^{30}$ $15^h$ (16+rd 25)
Krombach 15.9. $15^h$ (20) - 17.9. $6^{30}$ F
R
2.-3.10 (11)
15.9. (8)
Weilburg L. 17.9. (10) FR
Bischofsheim 16.9. $18^h$ (1)
17.9. (11) F
17.9. (8)
Lindheim 15.9. $15^h$ (82-85) - 17.9 $12^h$ FRR
Bad Orb 21.9 $15^{45}$ (1)
Neuhütten 19.9. $12^h$ (1)
Wertheim 17.9. (1)
R
17.9. abds - 22.9. (8-4)
F
17.9 $17^h$ F
18.9. $10^{50}$ (11)
Krautheim usw. 17.9. $16^{30}$ („100"!?) 18.9. 8-$12^{30}$ (19, 27, 60, 42, 30)
Jlshofen 18.-20.9. (1)
18.9. $18^h$ (4)
Beachte: Jllertal a) der Welle Krautheim vorauseilend!
Jllertal
a) 17.9. $15^h$ - 21.9. $17^h$ (30-20) F5R
b) 19-23.9. (52) RR
c) 24.9. (20), 5.10. (x)
28.9 (1) F
19.-23.9. (9-12) F
Penzberg 2.10 (1) F
Abtenau 16.9. $10^{30}$ (1) F
ab 25.9. (1) F
23.9. $15^h$ (60)
Kitzbühel 2.10 (1R)
24-25.9. (3) F
7.10. (1) F
24.9. (60-70)
23.-25.9. (1R)
Chur
25.9 (4)
24.9 (R)
Alpen
Visp 24.9. (1)
Lago Maggiore 24.9 (2R) 25.9. $10^h$ (50) (viele R)
Casalino 9.10. (1R)
Pavia 6.10. (5,1,4)
Corteolona 24.9 $17^h$ (5) 3 R
Acqui Ende 9. (1) 1.10 (4-5) F
Adria

Fig. 3. Wegzug von rd. 140 ostpreussischen Jungstörchen, die verspätet (12. September) 1933 in Essen aufgelassen wurden (Versuch 2 e). Die Hauptstrecke ist durch dicke schwarze Linie hervorgehoben. Die Mehrzahl der Störche, mehr als 100, verfolgten in Schüben die Richtung SE bis SSE, wurden durch den Lauf des Oberrheins im Gebirge abgelenkt, liessen sich aber trotz ungünstiger Witterung nicht von dem Hochgebirgsüberflug abhalten und verloren sich dann in Oberitalien. Die Angaben nennen Tag und Uhrzeit der Beobachtung, in Klammern die Stückzahl. F = Beobachtung der Farbkennzeichen, R = Ringstorch lebend oder tot angetroffen und abgelesen. (Umgezeichnet nach Schüz 1949.)

## I. Übersicht über die Versuche

### 1. *Versetzung von Gelegen*

a) Sturmmöwe, *Larus canus,* von Hiddensee nach Rossitten in den Biotop der Lachmöwe, *Larus ridibundus,* 1934. Von 79 beringten Sturmmöwen, die 500 km ostwärts vom Ablegeplatz ausgebrütet waren, kehrten (spätestens 1937) 5 (2 Ablesungen) zurück, um zu nisten; die zwei ersten Gelege 1938. Seither in dem für Sturmmöwen nicht geeigneten Teich regelmässig einige Bruten, wenn auch oft ohne Aufzuchterfolg, da offenkundig die Bedingungen in dem Gedränge der Lachmöwen ungünstig (Schüz 1938 a).

b) Stockenten, *Anas platyrhynchos*, aus England nach Rossitten 1936. 53 aus englischen Eiern erbrütete Jungenten am 19.8.36 ausgesetzt. Rückmeldungen westwärts bis Malmö, Seeland, Mecklenburg. Von Zurückgebliebenen 1937 reinblütiger Nachwuchs, der wandernd bis zu den Niederlanden nachgewiesen wurde; dazu 2 Heimkehrfälle (Putzig 1938 a).

### 2. *Verfrachtung von Jungvögeln* (*Weisser Storch*)

a) Aufzucht von rd. 50 Jungstörchen aus ostpreussischen Horsten (bis 133 km entfernt) in Rossitten, bei freier Haltung und unbehindertem Wegzug, 1926 bis 1942. Davon 7 in Rossitten später wieder aufgetaucht; 3 als Brutvögel. Gegenbeispiel ein Brutvogel am anderen Haffufer (49 km ESE vom Aufzucht- und 85 km ENE vom Schlüpfort) (Schüz 1943 a).

b) Aufzucht von 754 ostpreussischen Jungstörchen in mehr westlichen Teilen Deutschlands, Wegzug unbehindert, 1933 bis 1936. Siehe Fig. 1 und Unterschrift dazu (Schüz 1943 b, 1950 b).

c) Aufzucht von 23 ostpreussischen Jungstörchen in England und Schottland bei unbehindertem Wegzug, 1936. Die 19 in Kent aufgezogenen Störche pendelten nach dem Flüggewerden zwischen der Ostspitze und der Westspitze Englands hin und her. Auf der Insel Wight traf sich ein Teil mit einem der 4 Aufzuchtstörche von Dumfries-Shire. Erst am 7. Oktober wurde von Cornwall und der Insel Wight aus der Überflug gewagt; 2 Nachweise in der Bretagne gaben die letzte Kunde. Das Zögern an der Küste ist für einen den Zug über See scheuenden Gross-Segler bezeichnend (Schüz 1938 b).

d) Spät-Auflassung von 197 Jungstörchen aus Ostpreussen in Rossitten 1926, 1927, 1928, 1933. Die 12 Fernmeldungen weisen nur zum Teil an die bulgarische Küste; 4 Funde zielen auf Griechenland, 3 sogar nach dem östlichen Oberitalien. Im letzteren Fall (1933) hat die Buntfärbung das Erfassen (zumal in den besser überwachbaren West-Gebieten) stark begünstigt (Thienemann 1928, Schüz 1949).

e) Spät-Auflassung von 144 ostpreussischen Jungstörchen am 12. September 1933 in Essen (1010 km SW–WSW von Rossitten). Siehe Fig. 3 und Unterschrift dazu (Schüz 1949).

f) Spät-Auflassung von 20 ostpreussischen Jungstörchen am 12. September 1933 in Frankfurt a. M. (1 000 km SW von Rossitten). Wegzug nach

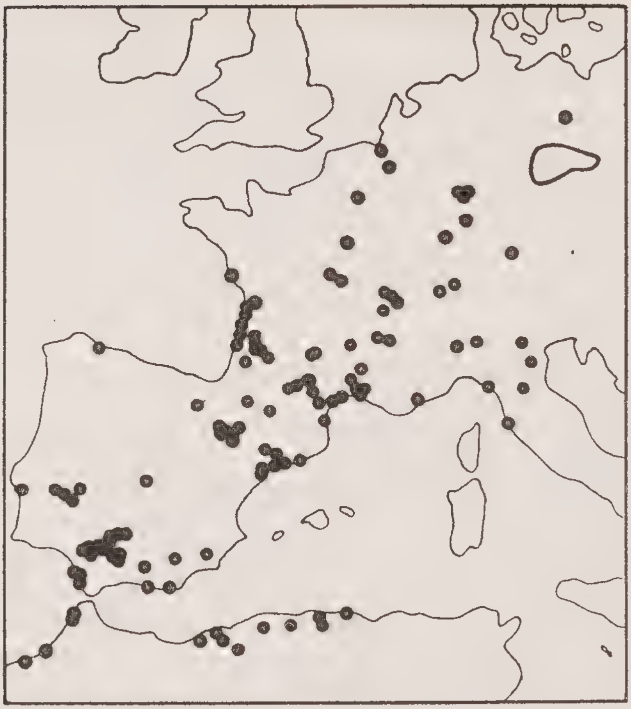


Fig. 4. Ringfunde sächsischer Stare (nach Krätzig und Schüz 1936).

SSE bis Hirschhorn am Knie des Neckars, von wo aus dann offenbar unter dem Einfluss des Oberrheintalgrabens die Richtung nach SW bis zum schweizerischen Mittelland eingeschlagen wurde. Ein Storch unvermittelt am 6.10. im Dép. Haute Marne (Schüz 1949).

### 3. *Versuche mit Durchzüglern*

a) Ostpreussische Zwischenzug-Stare — rd. 3 000 ganz vorherrschend junge Stücke — von der Windenburger Ecke am Kurischen Haff im Juni und Juli 1934 nach Breslau und Dresden. Siehe Fig. 4–7 und Unterschrift zu Fig. 7 (Krätzig und Schüz 1936, Schüz 1950 a).

b) Ostpreussische Frühjahrsdurchzügler der Nebelkrähe, *Corvus corone cornix,* — rd. 900 vorwiegend junge Stücke — vom Ostufer des Kurischen Haffs 1935, 1938 und 1939 nach Flensburg (750 km W), Essen (1025 km WSW) und Frankfurt a. M. (1010 km SW) verschickt. Siehe Fig. 8 und Unterschrift dazu (Rüppell 1944).

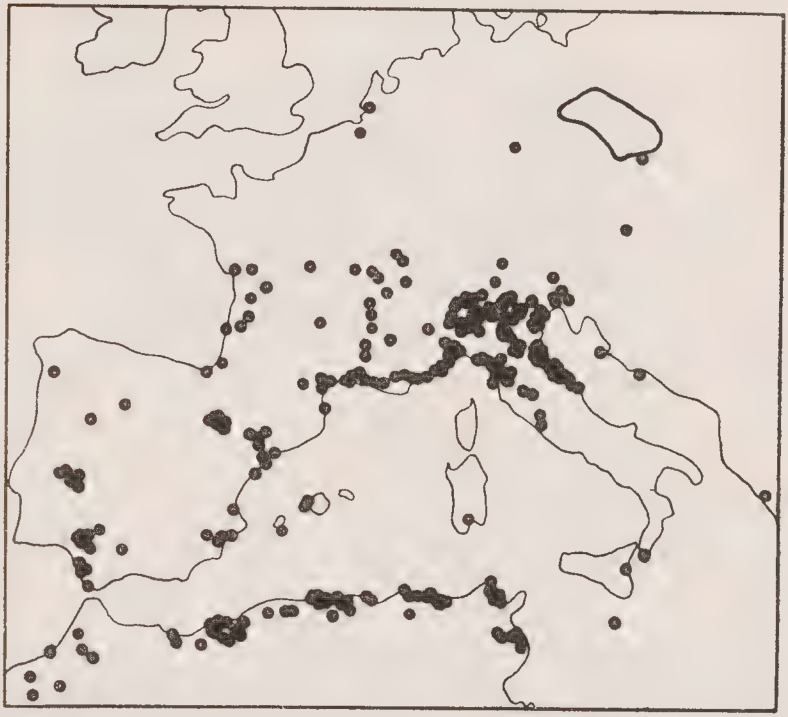


Fig. 5. Ringfunde schlesischer Stare (nach Krätzig und Schüz 1936).

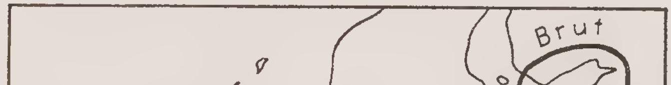


Fig. 6. Jahresverbreitung ostbaltischer Stare (nach Krätzig und Schüz 1936).

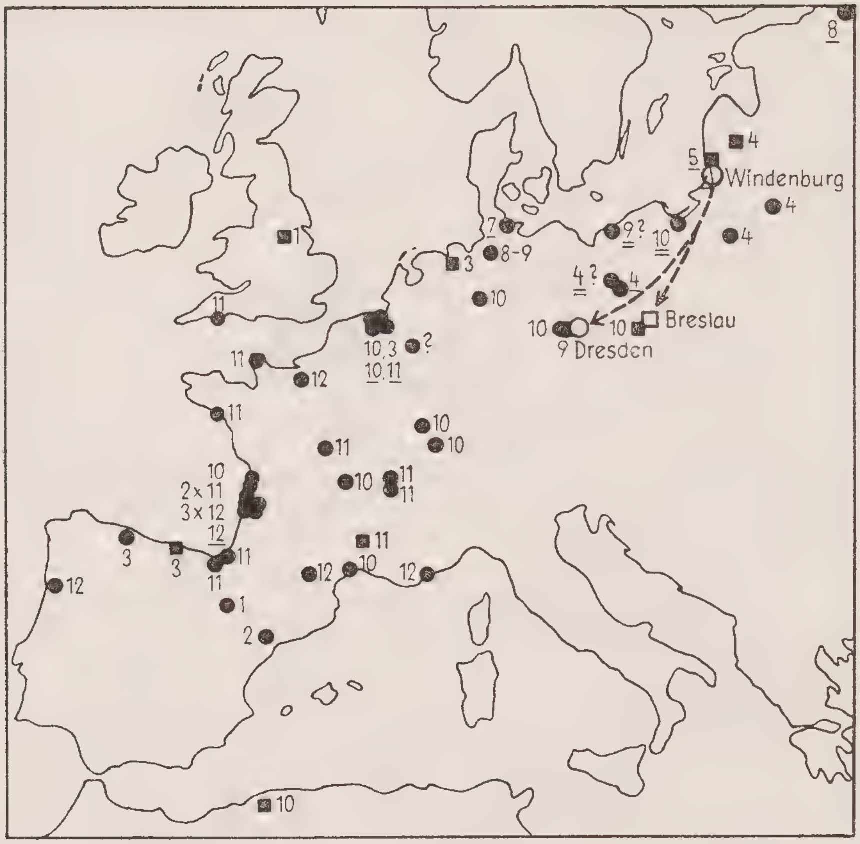


Fig. 7. Nachweise baltischer Stare, die als (meist junge) Zwischenzügler (Juni, Juli) vom Kurischen Haff (Windenburger Ecke) in Dresden (Kreise) und Breslau (Quadrate) freigelassen wurden (Versuch 3 a). Sie folgten den Staren des Gastlandes (Fig. 4, 5) nur bedingt, hielten sich im allgemeinen im Norden des sächsisch-schlesischen Stargebiets und wanderten grossenteils über die Nordgrenze hinaus, ja z. T. in das alte Areal der baltischen Stare (siehe Fig. 6) zurück.

c) Ostpreussische Herbstdurchzügler der Nebelkrähe — 238 vorwiegend junge Stücke — von Rossitten 1932 und 1934 nach Berlin (500 km WSW). Die Ergebnisse passen zu den in grösserem Masstab durchgeführten Frühjahrsversuchen (s. 3 b) (Rüppell und Schüz 1948).

d) Zwei Ergebnisse kastrierter Frühjahrs-Durchzügler (♂) der Nebelkrähe, die von Rossitten nach Berlin versetzt wurden (Putzig 1938 b, 1939 a [Karte] ), in Ergänzung zu Abflügen anderer Kastraten am Fangort: *Larus ridibundus, L. fuscus* (Putzig 1937), *Corvus corone cornix* (Putzig 1939 a,

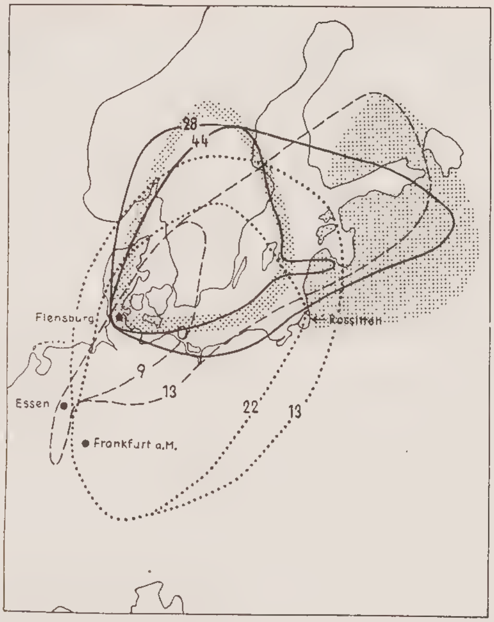


Fig. 8. Ostpreussische Frühjahrsdurchzug-Nebelkrähen (*Corvus corone cornix*) nach Versetzung 750, 1025 und 1010 km westwärts (Versuch 3 b). Ausbreitung im Sommerhalbjahr von Flensburg (ausgezogene Linie), Essen (gebrochene Linie) und Frankfurt a. M. (Punktlinie) aus. Der engere Kreis gibt die Ausbreitung im ersten, der weitere Kreis in den späteren Sommerhalbjahren (mit zugehörigen Fundzahlen), zum Vergleich mit der normalen Sommerverbreitung der ostpreussischen Küstendurchzügler (punktiertes Feld) und mit ihrer Verlagerung vom Kurischen Haff nach dem 750 km entfernten Flensburg (Feld mit punktierter Grenze). Es fand also eine Parallelverschiebung entsprechend der Verfrachtungsstrecke statt, zwar nicht in starrer Weise, aber doch in den wesentlichen Zügen. Diejenigen Vögel, die trotz der Verfrachtung zu ihrem östlichen Herkunftsraum zurückfanden, erwiesen sich, soweit kontrollierbar, zum grösseren Teil als Altvögel, die also in besonderem Masse auf entsprechende Erfahrungen zurückgreifen konnten. (Umgezeichnet nach W. Rüppell 1944.)

1939 b) und zu anderen physiologischen Versuchen (Hormon-Injektionen, Thyreoidea-Bestrahlung). Kastrierte ♂♂ der Nebelkrähe kehrten teilweise so weit nach dem NE (Lettland, Estland, Finnland bei Viborg) zurück, dass man das Erreichen des näheren Heimatgebietes für möglich halten muss.

### 4. *Verfrachtung brutbereiter oder brütender Vögel*

a) Star (*Sturnus vulgaris*).

a 1. 333 brutbereite Stare von Nistplätzen in der Nordhälfte Deutschlands März bis Mai 1934 bis Berlin (44 bis 465 bzw. 600 km weit) verschickt.

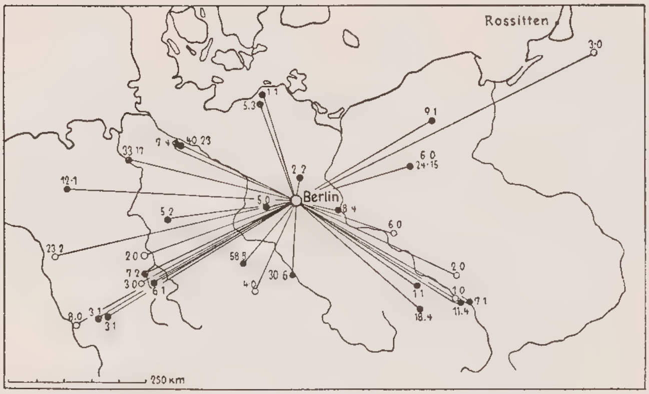


Fig. 9. Star-Versuch von W. Rüppell 1934. (Versuch 4 a 1, umgezeichnet nach Rüppell 1935.) Unter 353 Auflassungen brutbereiter Vögel vom Lande in Berlin 120 Wiederfunde und Wiederbeobachtungen am Heimatort. (Die Zahlen geben das Verhältnis der verschickten und der wiedergefundenen Stare an.) Da die Nistkasten in der Zwischenzeit meist wiederbesetzt und die Nachweise entsprechend schwierig zu führen waren, darf als sicher gelten, dass die wirkliche Heimkehrzahl bedeutend höher lag; wo besonders eifrig geprüft wurde, war die Zahl entsprechend hoch. Die Heimkehr erfolgte gemächlich; selbst bei Strecken von 200 bis 300 km geschah der Heimkehrnachweis frühestens im Lauf des übernächsten Tages (5 Fälle). Für Entfernungen von mehr als 300 km ist in 3 Fällen Heimkehr am 4. Tage nach der Auflassung als Bestzeit bekanntgeworden (320 und 360 km). Ob auf Kreisflügen oder gerichtet die Heimat angesteuert wird, konnte nicht entschieden werden. Ein von Wetzlar nach Berlin (405 km) verschickter Star wurde auf halbem Rückweg ziemlich nahe der Luftlinie tot gefunden, und ähnlich war es mit einem Star 1935, der halbwegs zwischen dem Auflassort Scheessel Bez. Bremen und dem 275 km entfernten Berlin näher an der Luftlinie (30 km) als an der benützten Bahnstrecke in einem Wanderfalkengewöll zum Nachweis kam. (Rüppell 1936 a S. 190, Versuch 4 a 2.)

Infolge Mehrfachsendungen 353 Auflassungen. Siehe Fig. 9 und Unterschrift dazu. (Rüppell 1935, 1936 a S. 198, 1936 b.)[1]

a 2. Weitere Star-Versendungen Rüppells April und Mai 1935 aus Winsen a.d. Luhe (Bez. Hamburg) nach Berlin (275 km), aus Winsen und aus Scheessel Bez. Bremen nach Malmö (306, 353 km) und nach Gleiwitz (671, 707 km). Auch diese Versuche brachten 53,6 % nachgewiesene Erfolgsfälle (Rüppell 1936 a–c).

a 3. Weitere Star-Versendungen Rüppells 1936 von Berlin nach München[2]

---

[1] Dazu kommt Star Helg. 649 274 o 22.4. 34 Mandern Bez. Kassel (Rüppell 1935 S. 485), aufgelassen in Berlin † erl. Nachricht 21.10. 37 nur 100 m vom Beringungsort.

[2] Dazu neu eine sichere Beobachtung nach Farbringen: o 26.4. 36 Berlin-Hohenschönhausen nach München, beob. Nachr. 21.2. 37 „während der starken Frostperiode“ Hohenschönhausen;

Venedig[1], Rom, Madrid[2], London, Kopenhagen[3] und Malmö.[4] 39 nach München geschickte Stare erbrachten 5 Heimkehrer, 63 nach Venedig keinen, 53 nach Rom 1, 24 nach Madrid 2, 26 nach London 4, 19 nach Kopenhagen 1 und 24 nach Malmö 4 Heimkehrer. Einer der Malmö-Heimkehrer (340 km) wurde am Wiederfangtag (15. Mai) nach München (500 km) gebracht und sang schon am 20. Mai 140 m vom früheren Nistplatz im Botanischen Garten in Berlin. Ein Vogel der Venediger Auflassung war am 9. Mai etwa auf halber Strecke 150 km östlich der Luftlinie in Oberösterreich gefunden worden (Rüppell 1937).

a 4. Versendung von 15 Staren, die 1 Jahr vorher als Nestjunge gekäfigt worden waren, Ende März 1937 von Winsen a. d. Luhe 114 km S nach Hannover durch W. Rüppell und W. Schein. Trotz eifrigster Nachsuche keine Rückkehrer entdeckt, wohl aber 3 als Totfunde bis zu 7 km nördlich vom Auflassplatz und einer als erlegt Ende August oder Anfang September 1,5 bis 1,8 km auch vom Auflassplatz. (Leider wohnt dem Versuch eine kleine Schwäche inne, weil die Vögel infolge eines Versehens eine Nacht und die ersten Frühstunden auf dem Bahnhof Hannover verbringen mussten, also nicht ohne weiteres als vollwertige Versuchsvögel gelten konnten) (Rüppell 1938).

a 5. Versendung von 30 Staren, die 1 Jahr vorher als Altvögel gekäfigt worden waren, am 6. April 1940 von Winsen nach Hannover. Von diesen Vögeln mit Aussenerfahrung wurden im gleichen Frühjahr nach der Auflassung 17 (= 57 %) am Heimatort wiedergefunden; kürzester Nachweis dauerte 3 Tage (Rüppell 1941).

ferner 275 859 o ad. ♂ 21.4. 36 Berlin-Lichtenberg, nach München † tot im Nistkasten (Junge flügge) Mitt. 15.6. 37 Hohenschönhausen.

[1] Zu dieser Venediger Auflassung gehören noch (neu!): 275 884 o ad. ♀ 21.4. 36 † erb. 21.10. 36 Mantua; *275 952* o ad. 26.4. 36 † erl. 24.10. 36 Venedig, am Lido; 284 116 o ad. ♂ 7.5. 36 † erl. 28.10. 36 Malo, Prov. Vicenza; 275 998 o ♀ 28.4. 36 † erl. 31.10. 36 Venedig, am Lido; 275 955 o ad. ♂ 26.4. 36 † 9.11. 36 Valli di Villimpenta, Pr. Mantua; 275 870 o ad. ♀ 21.4. 36 † erb. 17.11. 37 Capergnarnica, Cremona; 275 949 o ♂ 26.4. 36 † 3.12. 36 S. Martino dei Manzoli, Minerbio (Toschi 252, Bologna 1938).

Daraus geht (trotz der Spätjahrs-Daten) hervor, dass diese Stare nicht zurückgekehrt waren!

[2] Davon noch nicht veröffentlicht: *275 914* o 23.4. 1936 Berlin-Zehlendorf, Teltower Damm, am gleichen Abend freigelassen Madrid † 25.3. 38 Zehlendorf, Schreberstr. 4. Dazu neu: *275 933* o ♀ ad. 24.4. 36 Berlin-Dahlem, verschickt nach Madrid † capturada 22.5. 36 Carabanchel Bajo, 6 km von Madrid.

[3] Dazu neu: 284 135 o ad. 14.5. 36 Berlin-Dahlem, nach Kopenhagen † frisch erl. gef. 18.5. 39 Dahlem, Ecke Lans- und Iltis-Str. Ferner 284 185 o ad. ♂ 8.5. 36 Berlin-Lichtenberg † Mitt. 4.8. 37 Flughafen Kastrup.

[4] Neu: *276 017* o ad. 28.4. 36 Berlin, verschickt nach Malmö † 3.37 Malmö.

b) Schwalben (*Delichon urbica, Hirundo rustica*).

b 1. Verschickungen 1926 von Rossitten auf kurze Strecken. Rückkehrnachweis bis 11,6 km (Thienemann 1931).

b 2. Verschickungen Ende Juni 1934 von Pausin (bei Berlin) 390 bis 550 km westwärts. Innerhalb 4 Tagen von 21 Rauchschwalben 11 und von 6 Mehlschwalben 1 am Brutplatz wiedergefangen (und 1–2 (3) zusätzlich beobachtet) (Rüppell 1934).

b 3. Verschickungen 1935 von Winsen (Hamburg) und Scheessel (Bremen) nach London und Gleiwitz. Aus London (690 km) kehrten 5 von 7 Rauchschwalben und aus Gleiwitz (723 km) 4 oder 5 von 6 Mehlschwalben zurück. Von 14 bei London aufgelassenen Mehlschwalben nur 2–3 wiederbeobachtet, und zwar bei Gewittertätigkeit zur Zeit des Rückflugs. Die Höchstgeschwindigkeit von 400 km sank bei kaltem Wetter und Gegenwinden auf 150 km (Rüppell 1936 a).

b 4. Verschickungen 1936 von Berlin nach London, Athen und Madrid. Es kehrten zurück von London (900 km) 2 Rauchschwalben unter 8, von Athen (1 800 km) 2 unter 10 und von Madrid (1 850 km) ebenfalls 2 unter 10, bei günstigen sommerlichen Wetterlagen. Tagesleistungen bis zu 200 und 300 km (Rüppell 1937).

c) Rotrückenwürger (*Lanius collurio*).

12 Rotrückenwürger 1936 aus Berlin nach London, Amsterdam, Kopenhagen und Marseille. London (4 Versendungen), Amsterdam (4) und Kopenhagen (1) ohne Rückkehr, während von 3 nach Marseille (1 200 km) verschickten Würgern einer nach 11–13 Tagen zurückgekehrt war (Rüppell 1937).

d) Wendehals (*Jynx torquilla*).

19 Wendehälse 1936 mit Flugzeug von Berlin nach London, Kopenhagen, Malmö, München, Venedig, Rom und Saloniki. Es kehrten zurück von London[1] 2 unter 5, von Kopenhagen 0 unter 3, von Malmö 0 unter 1, von München 2 unter 4, von Venedig 1 unter 3, von Rom 0 unter 1, von Saloniki 1 unter 2; alles Brutvögel von einer Neuansiedlung in Dahlem (Rüppell 1937).

### 5. *Verfrachtung von Zugvögeln aus dem vermutlichen Winterquartier*

a) Von 78 im Dezember 1935 aus Berlin nach Luzern (700 km SW) verschickten alten Lachmöwen (*Larus ridibundus*) bis 21. Februar sicher

---

[1] Der 1936 aus London zurückgekehrte Wendehals *284 121* (Rüppell 1937 S. 130) wurde am 13.7. 37 als Sperberrupfung in Dahlem, am Grunewald, gefunden.

3 oder 4, wahrscheinlich aber 6 oder 7 nach Berlin zurückgekehrt. Eine dieser Wiederbeobachteten erneut, und zwar nach Radolfzell (600 km SW), versandt kehrte wiederum zurück. Abwesenheit (höchstens) 14 und 23 Tage. Von weiteren Versendungen nach Radolfzell (45 Möwen im Februar) keine Rückkehrer festgestellt. Aus beiden Gruppen ziemlich viel Berliner Wiederbeobachtungen im folgenden Winter (Rüppell und Schifferli 1939, Tettenborn 1943).

b) Von 52 Blässhühnern (*Fulica atra*), als Wintergäste im November und Dezember 1935 von Luzern nach Berlin verschickt, im gleichen Winter nur eines wieder bei Luzern festgestellt, von 31 Zürichern aber 6, die bezeichnenderweise alle bis auf einen Vogel einer Gruppe von 16 Stücken mit Gefiederkennzeichnung angehören. Wesentlich für den Erfolg ist also die Erkennungsmöglichkeit. Kürzeste Rückkehrdauer knapp 4 Tage (Rüppell und Schifferli 1939).

### 6. *Verfrachtung von Standvögeln*

Versendung von 19 Habichten (*Accipiter gentilis;* Fänge im Habichtskorb) aus der nördlichen Lüneburger Heide nach Radolfzell (Bodensee) und von 8 Habichten aus Niederschlesien nach Berlin und Essen. Die in der Fremde aufgelassenen Habichte breiteten sich bis zu 235 km aus. Die Heimkehr gelang noch auf 140, 200, 200 km, nach den neusten Funden ferner auf 300 und 600 km (Rüppell 1937, 1940, 1948).

## II. Folgerungen

A. Ist bei Versetzungen der alte Verbreitungszustand wiederhergestellt worden? — Ja, und zwar bei einer hohen Zahl von Verschickungen brütender oder brutbereiter Vögel, soweit Nachweise erzielt wurden (Star 4 a, Schwalben 4 b, Rotrückenwürger 4 c, Wendehals 4 d). Grenzen des Heimkehrvermögens beim Star nach Rüppell: Noch auf 707 km (Scheessel—Gleiwitz) kehrten 9 von 12 Staren zurück (4 a 2), auf 800 km (Berlin—Venedig) 0 von 63 (doch ist wenigstens ein Halbwegsfund erzielt), auf 900 km (Berlin—London) 4 von 26, auf 1 200 km (Berlin—Rom) 1 von 53, auf 1 850 km (Berlin—Madrid) 1, später 2 (Fussnote 2 auf S. 259) von 24 (4 a 3). Umsiedlungen bei der Verschickung nach Venedig ins Gebiet jenseits der Alpen sind offenkundig (siehe S. 259 Fussnote 1). Ein Berliner Star war nach Jahresfrist am Auflassplatz Malmö (Fussnote 4 auf S. 259). — Selbst Standvögel zeigen vereinzelt die Befähigung, über den bei ihnen üblichen Bewegungsradius hinaus die alte Heimat wiederzufinden. Habichte, deren Höchstentfernung in Deutschland nach bisheriger Kenntnis 170 km beträgt, sind auf 200, 200, 300 und 600 km Verfrachtung (nach Fang im Habichtskorb) in ihre Heimat zurückgelangt. Gegenbeispiel: 1 Habicht auch im Frühjahr noch am 600 km entfernten Auflassort (Niederschlesien nach Essen) (6). — Sogar vom Kurischen Haff nach Breslau und Dresden versetzte Zwischenzug-Stare (junge und vereinzelte alte) schlossen sich nur bedingt den Staren des Gastgebiets an (Fig. 7). Sie drängten bis auf wenige Ausnahmen in den Norden des Winterquartiers der Sachsen und Schlesier und fanden sogar zu einem grossen Teil darüber nordwärts hinaus, offenbar in Einzelfällen selbst in das alte baltische Verbreitungsgebiet (3 a).[1] — Auch Überwinterer können sich wenigstens vereinzelt an ihren Winterplätz zurückwenden. Von 78 Wintergästen der Lachmöwe, die im Dezember von Berlin nach Luzern verschickt worden waren, kehrten nachweislich 3–4, wahrscheinlich aber 6–7 bis 21. Februar zum ersten Fangort zurück. (Gegenbeispiele: Mehrere am neuen Winterplatz (Seen der Schweiz) verbliebene Lachmöwen und ein nach Barcelona weiterschweifendes Stück (5 a).) Von 31 Züricher Winter-Blässhühnern, die Ende November und im Dezember nach Berlin verschickt worden waren, wandten sich 6 bald wieder nach Zürich zurück (5 b).

B. Haben sich die Versuchsvögel bei Verfrachtung dem Platzwechsel angepasst? — In besonderen Fällen: Ja. Nämlich: Sturmmöwen, die 500 km weit W→E im Ei verfrachtet und von Lachmöwen an einem für *canus* nichttypischen Brutplatz aufgezogen worden waren, behielten wenigstens zu einem kleinen Teil den Aufzuchtort als Brutplatz bei (Gegenbeispiel: keines), obwohl sie jeweils den Winter über abwesend waren (1 a). Über in ähnlicher Weise verpflanzte englische Stockenten können so genaue Angaben nicht gemacht werden (1 b). — Junge Weiss-Störche, in Rossitten bis zu 133 km vom Heimatnest entfernt aufgezogen, wählten mindestens in kleiner Zahl den Aufzuchtort als späteren Brutplatz. (1 Gegenbeispiel, aber bei dieser Ansiedlung Aufzucht- und Herkunftsnest 49 und 85 km entfernt) (2 a). Von 754 ostpreussischen Jungstörchen, die in fremdem Populationsgebiet weit westwärts (die meisten rd. 1 000 km entfernt) aufgezogen worden waren, schloss sich die Mehrzahl der westlichen Schmalfront an (Fig. 1) und verblieben wenigstens 6 im Westen: 5 wurden als Heimkehrer angetroffen, 1 brütete 120 km vom Aufzuchtnest entfernt. Keine Gegenbeispiele bis auf einen in Bulgarien vorgefundenen Heimkehrer (2b). Ostpreussische Jungstörche, die verspätet in Westdeutschland aufgelassen wurden, hielten sich grösstenteils sehr genau an die populationseigene Richtung und scheuten auch den Vorstoss in die im Weg liegenden Alpen nicht (2e, siehe Fig. 3). — Die als Heimzügler vom Kurischen Haff 750 bis über 1 000 km westwärts versetzten Nebelkrähen zeigten eine „nichtstarre Parallelverschiebung" (W. Rüppell) des Verbreitungsgebiets, so dass beispielsweise der Scheitel der Sommerverbreitung dieser Versuchsvögel nach Schweden anstatt nach Finnland fiel (3b, siehe Fig. 8).

---

[1] Auch Helgoländer Märzdurchzügler des Stars (wie alt?), 1934 nach Schlesien verfrachtet, strebten in bemerkenswerter Weise in Richtung Heimat zurück (Funde in Mecklenburg und auf Seeland). (R. Drost, Proceedings Eighth Int. Orn. Congr. Oxford 1938.) Ein gross angelegter Versuch mit Sperbern (*Accipiter nisus*), die als Herbstdurchzügler 1933 bis 1937 von Helgoland nach Schlesien verschickt wurden, zeigten ebenfalls recht eindeutig Richtungsgebundenheit bei Jungvögeln und Zurückdrängen zum alten Lebensraum bei Altvögeln (R. Drost, IXme Congr. Orn. Int. Rouen 1938; Rouen 1938). Es handelt sich hier also um eine möglicherweise verbreitete Regel.

C. Heimkehrgeschwindigkeiten bei Rückkehrern nach der Verfrachtung. Soweit Art und Zeitpunkt der Wiederbeobachtung Rückschlüsse zulassen, haben die Vögel stets wesentlich länger gebraucht, als dem unmittelbaren Flug entsprechen würde. Bei Schwalben (siehe 4b 2) war die Tages-Höchstgeschwindigkeit 120 km (tatsächlich wohl 150 km? Rüppell 1936 a). Sie sind also nur mit Verzögerung oder auf grossen Umwegen geflogen. Die wenigen Zwischenstreckenfunde (z. B. an Rüppellschen Staren) liegen allerdings mehr oder weniger nahe der Luftlinie, in dem Österreich-Fall abgewandt von der Verfrachtungsstrecke (4a 1, 4a 2, 4a 3).

D. Erfahrung ein ausschlaggebender Faktor? Viele Beispiele sprechen dafür, dass alte Vögel, die schon einmal ihren Wegzug und Heimzug gemeistert haben, im Erreichen ihrer Heimat erfolgreicher sind als unerfahrene. Wahrscheinlich ist die Erfahrung von ausschlaggebendem Gewicht beim Erreichen eines früher bewohnten Raumes, der etwa anlässlich des Flüggewerdens „gelernt" werden musste (4a 4, 4a 5). Diesem Befund kann gegenübergehalten werden, dass die erstmals wegziehenden Vögel, auch bei den nicht geselligen Arten, gleich ob Tag- und Nachtzügler, ihre Aufgabe ebenfalls bewältigen. Die Versuche haben deutlich gemacht, dass der Geselligkeitstrieb bei gewissen Arten diese zweifellos vorhandene Befähigung überdeckt (2b gegenüber 2e). Die Antwort kann also nur lauten: Wichtig ist Erfahrung und angeborene Befähigung — diese aber in einem stärkeren Ausmass, als man bisher angenommen hat.

E. Bezogenheit zu einem Ziel oder zu einer Himmelsrichtung? Die „nichtstarre Parallelverschiebung" beim Verhalten der versetzten Nebelkrähen (3b und c, Fig. 8) und Rowans ganz entsprechender Befund bei *Corvus brachyrhynchus* in Nordamerika bekunden recht eindeutig, dass hier eine bestimmte Himmelsrichtung aufgenommen wurde; es sind offenbar (fast) allgemein nur die erfahrenen Altvögel, die sich nicht verführen lassen und in einer Anzahl von Fällen in die alte Verbreitung zurücksteuern (vgl. auch 3 a). Angeboren wäre hier also das Ansprechen auf eine bestimmte Himmelsrichtung. Die nach Sachsen und Schlesien verbrachten baltischen Stare (3 a) gaben sich den Anschein, als ob sie grossenteils in ihre alte Jahresverbreitung zurückgezielt hätten (Fig. 7). Doch ist das Hineingeraten der Versuchsvögel in ihr altes Gebiet auch schon dann erklärlich, wenn sie ihrer Herkunft entsprechend stärker westwärts hielten als die Stare des Gastlandes, da sie so mit dem südlichen Arm der baltischen Starscharen in Verbindung kommen mussten. Die Storchversuche sind insofern nicht leicht auszuwerten, als bei der riesigen Weite des Zugwegs eine Versetzung um nur 1 000 km westwärts keine deutlichen Winkel-Abweichungen erwarten lässt. Nimmt man indes an — wofür manches spricht — dass die Zugstrecke des Storchs durch eine Anzahl Zwischenziele aufzugliedern ist, so steht fest, dass die verfrachteten Ostpreussen-Störche nicht etwa zum Bosporus oder zum Golf von Iskenderun „zielten", sondern dass sie in der Hauptsache ihre (erste) populationseigene Himmelsrichtung nach SSE einhielten (2 e, Fig. 3) (soweit sie nicht unter den Einfluss wegziehender Weststörche gelangten, 2 b, Fig. 2). Eine wesentliche Erkenntnis ist die, dass die Wegzügler nicht eine ganz allgemeine Richtung einhalten, sondern mindestens in manchen Fällen auf einen recht engen Zugwinkel eingewiesen sind. — Im Gegensatz zu diesen Befunden stehen die zur Brutzeit verschickten Stare u. a. Vögel, soweit zurückfindend, denn sie erwecken den Eindruck der Zielbezogenheit (4, Fig. 9). Die Prüfung der Fundzahlen und der wenigen Zwischenfunde macht glaubhaft, dass hier nicht, wie offenbar bei den Tölpeln nach Griffin und Hock, nur ein Spielen und Tasten in Frage kommt — wenn auch die lange Heimkehrdauer diese Deutung begünstigt —, sondern dass viele Vögel mit einer gewissen Sicherheit vorgehen. — Himmelsrichtung oder Ziel? Die erstere Lösung kann für eine Reihe von Fällen als gesichert gelten, doch kann vorläufig (für andere Fälle) auch die zweite nicht von der Hand gewiesen werden.

F. Damit kommen wir zu den Schlüssen auf die den Weg bestimmenden Kräfte. Sicher ist, dass ein höheres Mass bestimmter Leitung vorliegt, als man eine zeitlang annahm. Diese Leitung kann 1. durch erfahrene oder (im Verhältnis zu den Versuchsvögeln) sich jedenfalls „sicher" fühlende Artgenossen erfolgen, soweit die Art gesellig zieht (und zwar vor allem am Tage). Diese Bedingung ist gewiss manchmal erfüllt, wenn auch nicht allein ausschlaggebend (2 b). — 2. Die Landschaftsformen, besonders die ökologischen Leitlinien, können bei manchen Arten eine sehr wesentliche Rolle spielen; besonders bei Küstenzüglern. Es ist aber sicher, dass auch dieser Faktor selbst bei den ausgesprochenen Vertretern dieser Gruppe zur Deutung nicht ausreicht. Die Wirksamkeit ist manchmal mehr negativer Art, so wie beim Storch, für den grosse Wasserflächen abweisend wirken (2 c). — 3. Kinästhetische Registrierungen scheiden aus, nicht nur nach experimentellen Ergebnissen (z. B. Drehversuche beim Versand von Staren, 4 a 2), sondern auch, weil der erstmals wegziehende Vogel auf diese Art Erfahrung nicht zurückgreifen kann. — 4. Mannigfaltig sind die Überlegungen und Versuche, die von den verschiedensten Seiten über die vom Vogel bei der Zugorientierung verarbeiteten Aussenreize angestellt wurden. Trotz mancher Befürwortungen hat ein Ansprechen auf gewisse Kräfte von minimalem Absolutwert und minimalem Gefälle (erdmagnetisches Feld, Schwerkraft, Coriolis-Effekt) mehr und mehr an Wahrscheinlichkeit verloren (vgl. G. Kramer 1948 u.a. gegen H. L. Yeagley). Es bleibt am ehesten eine Art Lichtkompass übrig. Obwohl es eine erstaunliche Zeit-Kontrolle und den triebmässigen Vollzug der tages- und jahreszeitlichen Korrekturen voraussetzt, kann das Bestimmen der Zugrichtung auf Grund des Sonnenstandes beim Star als erwiesen gelten, und zwar durch die hervorragenden Versuche G. Kramers (siehe diese Kongressberichte). Damit wäre das Richtungnehmen des Wegzüglers begreiflich gemacht, noch nicht aber das Zurechtfinden des im Experiment versetzten Vogels. Es fehlt hier der für das Achsensystem notwendige Partner-Wert zum Sonnenstand, es sei denn, es würde der Vertikalwinkel der Sonne empfunden und die Versetzung wäre in meridionaler Richtung erfolgt. Es sei hier festgehalten, dass die Versuche bisher keinen Anhaltspunkt für grösseren Heimkehrerfolg von Meridional- gegenüber den Latitudinal-Verfrachtungen ergaben. —

G. Zum Schluss muss eine besondere Eigentümlichkeit der Zugvogelorientierung in ihrem Verhältnis zu anderen Orientierungsvorgängen zur Sprache gebracht werden. Die klassischen Richtungshandlungen, die Taxien Alfred Kühns, sind bekanntlich dem Wesen nach angeborene, im Einzelablauf sinnesphysiologisch gelenkte Vorgänge, die meist über Arten und Gattungen hinweg recht gleichartig aussehen. Es ist nun der Zugvogel-Fernorientierung eigen, dass vielfach nicht nur von Art zu Art, sondern sogar schon von Population zu Population beträchtliche Abweichungen vorkommen können. Da es nicht wahrscheinlich ist, dass verschiedene Populationen einer Art verschiedenartige Aussenreize aufnehmen, muss eine nach Populationen verschiedene Verarbeitungsweise angenommen werden. — Man denke an die Vorgänge bei einer grundsätzlich andersartigen Gruppe ererbter Handlungen, nämlich bei den Instinktbewegungen, wo zwischen die Aussenwelt und die innerste Befehlsstelle (aber ebenfalls schon im Zentralvervensystem) der auslösende Mechanismus (das auslösende Schema) eingebaut ist, dessen Wahlfunktion biologisch die grösste Bedeutung hat und gewissermassen den endogenen Automatismus vor Vergeudung schützt. Bei den Richtungshandlungen gibt es zwar keine solche Abschirmung (wenn man von der hormonalen Bedingtheit der die Ausführung voraussetzenden Appetenz absieht), wohl ist aber ein Mechanismus der Winkelkorrektion anzunehmen, der art- und sogar populationsverschieden sein kann!! Dieses Postulat lässt erneut klarwerden, wie hochentwickelt und verwickelt diese Vorgänge sein mögen, in einer durchaus eigentümlichen und ganz anderen Weise, als die — erfahrungsgebundene — Mnemotaxis das Bild der ,,einfachen" Taxien abwandelt.

Wenn wir schon — mit aller Vorsicht — Vergleiche mit dem nicht verwandten Gebiet der endogenen Automatismen ziehen, so wäre noch der Einwand zu würdigen, ob hier nicht modifikatorische Prägungen vorliegen können, wie sie K. Lorenz für den Begriff des Elternkumpans nachgewiesen hat. Eine solche Prägung in frühester Jugend und ,,auf den ersten Blick" ist auch durch unsere Versuchsreihe 1 a kaum zu erweisen. Es gibt aber einen sehr wesentlichen Gegengrund theoretischer Art. Es genügt sicherlich oft nicht, wenn dem wegziehenden Jungvogel nur die erste Wegzugrichtung als angeboren unterstellt wird. Auch das Ansprechen auf spätere Signale muss vorbereitet sein. Wenn wir die Verwicklung in den Zugwegen so mancher Arten und Populationen bedenken, so erhebt sich zwingend die Forderung, dass z. B. beim Zug der Oststörche gewisse Wendepunkte innerlich ,,bereitliegen". Auch bei anderen ,,Hakenzüglern" ist es immer unwahrscheinlicher geworden, dass Artgenossen oder dass ökologische Faktoren der Landschaft die ganz ausschlaggebenden Lenker sind. Es ist kaum anders denkbar, als dass vielen Vögeln nicht nur ziemlich genaue Richtungen angeboren sind, sondern auch, dass diese Richtungen wechseln und dass gewisse Landschaftsformen dabei (nicht jederzeit, aber vielleicht nach Ablauf einer bestimmten Leistung) eine Signal-Bedeutung haben können. Es muss also bei den Arten mit Hakenzug dem einzelnen Vogel — als Vertreter seiner Population — ein Komplex von Besonderheiten innewohnen, die nicht durch eine von aussen kommende Prägung während der Ontogenese gewonnen sein können.

In ,,Vogelzug" 2/1931 S. 19–28 gaben wir einen Abriss der Orientierungsversuche nach dem Stand von 1930. In den zwei seither verflossenen Jahrzehnten haben sich unsere Erfahrungen über Art und Bedingung des Sichzurechtfindens der Vögel gegenüber damals beträchtlich erweitert. Zu den hier überblickten Versuchen der Vogelwarte Rossitten und W. Rüppells sind weitere planmässige Reihen auf Seiten anderer Vogelwarten und anderer Untersucher getreten. Besonders hervorgehoben seien die Arbeiten Donald Griffins in Nordamerika. Der entscheidende Fortschritt ist aber im Laboratorium erzielt worden, und zwar durch G. Kramer. Für die Erforschung des in unserem letzten Abschnitt angedeuteten, besonders wichtigen Problems der „angeborenen Landschaftsmerkmale“ wird es auch weiterhin eines Zusammenspiels von Aussen- und Innenversuchen bedürfen, wobei die Fortentwicklung der Technik früher verschlossene Wege öffnen kann.

## Literaturverzeichnis

Krätzig, H., und Schüz, E., 1936. Ergebnis der Versetzung ostbaltischer Stare ins Binnenland. Vogelzug 7: 163–175.

Putzig, P., 1937. Beziehungen des Zugablaufs zum Inkretdrüsensystem. Vogelzug 8: 117.

— 1938 a. Über das Zugverhalten umgesiedelter englischer Stockenten. Vogelzug 9: 139–145.

— 1938 b. Weitere Versuche über die Beziehungen der Keimdrüsen zum Zugverhalten. Vogelzug 9: 189.

— 1939 a. Keimdrüsen und Heimzug. Ber. Ver. Schles. Orn. 24: 36-41.

— 1939 b. Sechste Rückmeldung einer kastrierten Nebelkrähe in Heimzugrichtung. Vogelzug 10: 171.

Rüppell, W., 1934. Heimfindeversuche mit Rauchschwalben (*Hirundo rustica*) und Mehlschwalben (*Delichon urbica*) von H. Warnat (Berlin—Charlottenburg). Vogelzug 5: 161–166.

— 1935. Heimfindeversuche mit Staren 1934. J. Orn. 83: 462-524.

— 1936 a. Heimfindeversuche mit Staren und Schwalben 1935. J. Orn. 84: 180-198.

1936 b. Nachträgiche Einzelergebnisse der Star-Verfrachtungen 1933–1935. Vogelzug 7: 140, 141.

— 1936 c. Neuansiedlung eines fernverfrachteten Stares in 12 km Entfernung vom ursprünglichen Brutplatz. Vogelzug 7: 204.

1937. Heimfindeversuche mit Staren, Rauchschwalben, Wendehälsen, Rotrückenwürgern und Habichten. J. Orn. 85: 102–135. (Dazu Fussnoten hier S. 258-260.)

— 1938. Ergebnis eines Heimfindeversuchs mit aufgezogenen Staren. Vogelzug 9: 18.

— 1940. Neue Ergebnisse über Heimfinden beim Habicht. Vogelzug 11: 57–64.

— 1941. Über das Heimfinden freilebender Stare bei Verfrachtung nach einjähriger Freiheitsentziehung am Heimatort. Vogelzug 12: 49–56.

— 1944. Versuche über das Heimfinden ziehender Nebelkrähen nach Verfrachtung. J. Orn. 92: 106–132.

— 1948. Heimkehr verfrachteter Habichte aus 300 und 600 km Entfernung. Vogelwarte 15: 39.

Rüppell, W., und Schifferli, A., 1939. Versuche über Winterortstreue an *Larus ridibundus* und *Fulica atra* 1935. J. Orn. 87: 224-239.

Rüppell, W., und Schüz, E., 1948. Ergebnisse der Verfrachtung von Nebelkrähen während des Wegzugs. Vogelwarte 15: 30–36.

Schüz, E., 1938 a. Über künstliche Verpflanzung bei Vögeln. IX. Congr. Orn. Int. Rouen 1938: 315–318.

— 1938 b. Auflassung ostpreussischer Jungstörche in England 1936. Vogelzug 9: 65–70.

Schüz, E., 1943 a. Vierzehn Jahre Storchsiedlung Rossitten. Vogelzug 14: 90–109.

—— 1943 b. Versuche über die Bindung des Storchs an seinen Aufzuchtort. Vogelzug 14: 137–141.

—— 1949. Die Spät-Auflassung ostpreussischer Jungstörche in Westdeutschland 1933. Vogelwarte 15: 63–78.

—— 1950 a. Verfrachtete Zwischenzug-Stare kehren zum Teil in das Gebiet ihrer Jahresverbreitung zurück. Vogelwarte 15: 192–194.

—— 1950 b. Früh-Auflassung ostpreussischer Jungstörche in West-Deutschland durch die Vogelwarte Rossitten 1933–1936. Bonner Zoologische Beiträge 1: 239–253.

Tettenborn, W., 1943. Feststellungen an beringten Lachmöwen in Berlin, Winter 1942/43. J. Orn. 91: 286–295.

Thienemann, J., 1928. »Rossitten«, 2. Aufl. Neudamm 1928.

—— 1931. Vom Vogelzuge in Rossitten. Neudamm 1931: 53–56.

# Eine neue Methode zur Erforschung der Zugorientierung und die bisher damit erzielten Ergebnisse

*Gustav Kramer*

*Max Planck-Institut für Meeresbiologie, Wilhelmshaven*

Das Orientierungsproblem hat sich bis vor kurzem dem direkten experimentellen Zugriff völlig entzogen. Die Gründe dafür sind rein praktischer Art: Die Distanzen, um die es sich dabei handelt, sind nicht in einem kontrollierten Versuchsfeld unterzubringen.

Neuerdings wurden nun 2 Wege beschritten, um eine Annäherung an den fliegenden Vogel zu ermöglichen. Den einen machte sich Griffin zu eigen: Er folgt seinen Versuchsvögeln im langsam fliegenden Flugzeug. Diese Methode eignet sich vorwiegend für das zweifellos kompliziertere Heimfindeproblem, wurde auch von Griffin in diesen Sinne verwendet.

Seit einigen Jahren bin ich mit meinen Mitarbeitern dabei, eine andere Methode auszuarbeiten, mit dem Ziel, die Zugorientierung gewissermassen laboratoriumsreif zu machen. Das methodische Prinzip besteht darin, dass die Richtungstendenzen bei den Bewegungen des gekäfigten Zugvogels registriert werden. Infolge der räumlichen Beschränkung des Vogels besteht dann die Aussicht, die physikalischen Bedingungen zu variieren, denen der Vogel ausgesetzt ist.

Die Brauchbarkeit der Methode wurde zuerst an nächtlich ziehenden Arten, hauptsächlich Grasmücken (*Sylvia*) erwiesen. Wir fanden dann, dass die Tagesaktivität des Stars sich gut für unsere Methode eignete. Was ich heute vortrage, bezieht sich nur auf den Tagzug des Stares. Es ist freilich wahrscheinlich, dass die Ergebnisse auf andere Tagzieher ausgedehnt werden können.

Drei unserer vier Volierenstare (Vögel vom gleichen Jahr) begannen am 6. Oktober in ruheloser Aktivität in die SW-Ecke ihres Käfigs zu drängen. Zwei davon übertrugen wir daraufhin in einem grossen Rundkäfig (5 m Durchmesser), der so aufgestellt war, dass die Horizontsicht verwehrt war. Die ringsum führende Sitzstange erlaubte den Staren, ihre Richtungstendenz in sehr genau bestimmbarer Weise zu zeigen: Sie wies nach SW.

Wir bemühten uns, die Unabhängigkeit der Orientierung von Landschaftsmarken noch einwandfreier zu erweisen. Wir gewöhnten einen der zwei übriggebliebenen Vögel an unsere Rundkäfige von 70 cm Durchmesser, welche eine ambulante Beobachtung möglich machten: Wir führten den Vogel in optisch voll verdecktem Käfig an möglichst verschiedene Landschaftpunkte, befreiten ihn dort von seiner Hülle und stellten die vom Star angestrebte Himmelsrichtung fest. Viele der Beobachtungspunkte ermangelten der Horizontsicht. An manchen dieser Stellen ohne Horizontsicht war ausserdem das erdmagnetische Feld durch schwere Eisenmassen so stark entstellt, dass die Kompassnadel völlig unzuverlässig wurde.

Unsere Herbstbeobachtungen hatten das Gesamtergebnis, dass alle abgelesenen Richtungen mit der natürlichen Zugrichtung der Art in Einklang standen. Unbeeinflusste Beobachter, die vorsichtshalber herangezogen wurden, machten die gleichen Feststellungen wie ich selber. — Darüber hinaus lagen die Einzelbestimmungen eines Tages, ja mehrere Tage hintereinander, so nah beieinander, dass wir sicher waren, über eine solide Grundlage für experimentelle Eingriffe zu verfügen.

Während demnach die herbstlichen Richtungstendenzen übereinstimmen mit den Zugrichtungen des Stars, wie sie von den Vogelwarten festgestellt wurde, konnte man dies für die Frühjahrstendenzen nur für die Periode 8.–18. III. behaupten, in der nördliche bis östliche Tendenzen sowohl im feststehenden Rundkäfig als auch bei ambulanten Richtungsbestimmungen festgestellt wurden. Von da an tendierte der Star nach NW.—

Wir enthalten uns einer Erklärung für diese ,,falsche“ Zugrichtung. Wir bedienen uns ihrer einfach als eines Indikators, um Auskunft zu erhalten über die Wirkung experimenteller Eingriffe. Was hierfür zu fordern ist, ist lediglich ein genügendes Mass von Richtungskonstanz, wie sie der Vogel in seiner NW-Periode in geradezu idealer Weise bot.

Nachdem andere physikalische Bedingungen schon weitgehend an Wahrscheinlichkeit als richtende Faktoren eingebüsst hatten, blieb als Aussichtsreichste Hypothese die einer Orientierung nach optischen, am Himmel gelegenen Merkmalen übrig. Unser Plan war der, den exakten Nachweis dadurch zu erbringen, dass wir den Vogel durch Spiegel von seiner spontan gewählten Richtung ablenkten. Zu diesem Zweck war es nötig, das Gesichtsfeld bis auf ein technisch handliches Mass zu reduzieren: Der Vogel wurde in seinem trommelförmigen Rundkäfig in einem Pavillon aufgestellt, in dem nur der Ausblick auf 6 Himmelsausschnitte von bestimmter Grösse ermöglicht war (Fig. 1, 2).

Glücklicherweise kam unser Versuchs-Star uns noch darin entgegen, dass er durch Selbstdressur seine Bewegungen im Käfig zeitweise erheblich diszi-

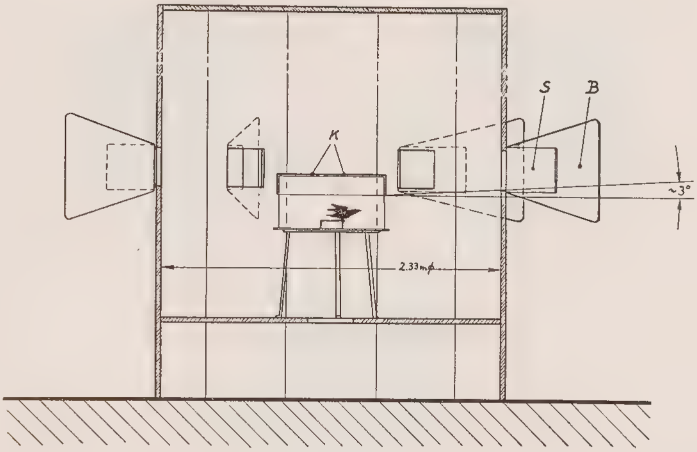


Fig. 1. Massstabgerechter Aufriss des Versuchspavillons. In der Mitte der trommelförmige Versuchskäfig mit Star. Die höchste Stelle, von der aus der Star Sicht nach aussen gewinnen kann, ist durch eine undurchsichtige, dem Käfig aufliegende Kappe (k) gegeben. Auch von ihrer unteren Kante aus ist der Horizont nicht sichtbar. Unter dem Versuchskäfig die kreisförmige Bodenluke, durch welche beobachtet wird. — S = Spiegel. B = dahinter montierte Blende, welche die Sicht des nicht gespiegelten Himmels verwehrt. — Vgl. auch Fig. 2.

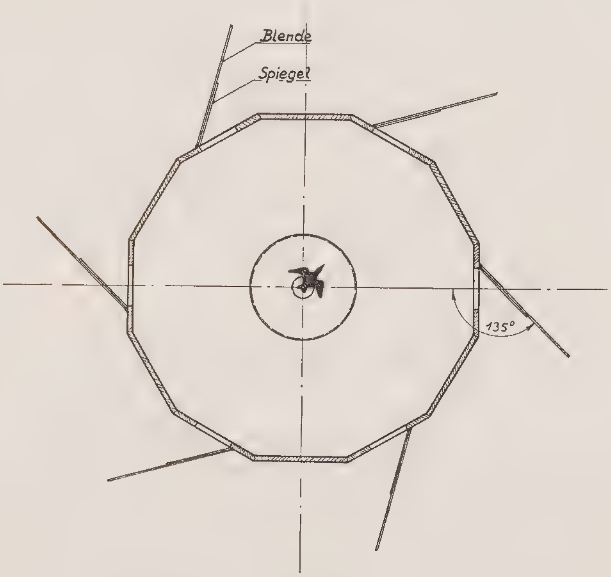


Fig. 2. Massstabgerechter Grundriss des Versuchspavillons.

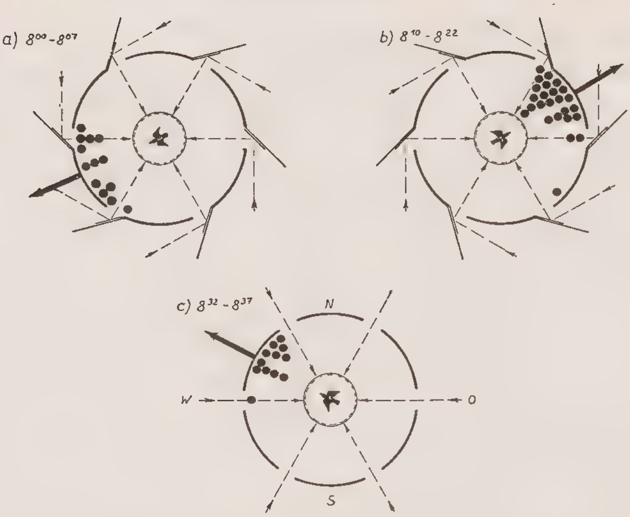


Fig. 3. Ablenkung der Zugtendenz des Stars. a): Im Gegen-Uhrzeigersinn bei Spiegelstellung »A«; b): dasselbe im Uhrzeigersinn bei Spiegelstellung »B«; c): Grundtendenz ohne Spiegel. Die dicken Pfeile, welche die resultierende Mittelrichtung des Vogels angeben, wurden durch Vektorenrechnung gewonnen.

plinierte und uns gestattete, die von ihm innegehaltene Richtung in Registrierperioden von 3–5 Minuten genau genug festzulegen. Er fusste dabei auf dem zentral angebrachten Sitzring seines Käfigs und schwirrte manchmal über längere, in anderen Fällen über kürzere Perioden nach der Richtung seiner Tendenz. Dabei pendelte seine Längsachse innerhalb eines Winkelbereichs von 90° hin und her. Die Feststellungen wurden dadurch quantitativ gestaltet, dass über jeweils 10 Sekunden integrierend abgelesen wurde. Die einzelnen Punkte auf den Diagrammen Fig. 3, 4 u. a. geben solche Einzelablesungen wieder. Etwas langwieriger ist die Ablesung dann, wenn der Star nicht „schwirrt", sondern seine Richtungstendenz durch Anrennen und Anspringen an die Wand kundtut.

Ich hoffe, das Prinzip der Methode mit genügender Anschaulichkeit vermittelt zu haben und schreite zur Mitteilung der Ergebnisse.

Aus dem bisher gezeigten geht schon hervor, dass der Vogel tatsächlich auch unter den Bedingungen der reduzierten Himmelssicht gerichtete Aktivität entfaltet. Wir betrachteten dies als einen Glücksfall und konnten zur Anwendung der Spiegel schreiten.

Wir erhielten diejenige Ablenkung, die zu erwarten war, wenn der Vogel sich nach der Einfallsrichtung von Lichtstrahlen orientierte (Fig. 3). Abweichungen von der theoretisch zur erwartenden Ablenkung um 90°

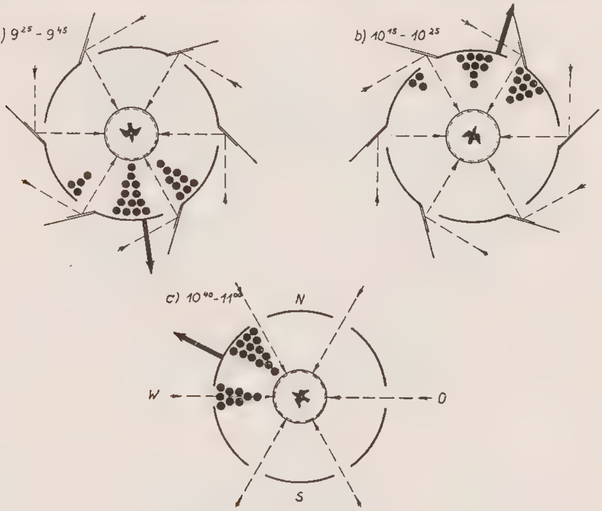


Fig. 4. Übertriebener Ablenkungseffekt bei Spiegelstellung A (a); erwartungsgemässer Effekt bei Spiegelstellung B (b); Grundrichtung (c).

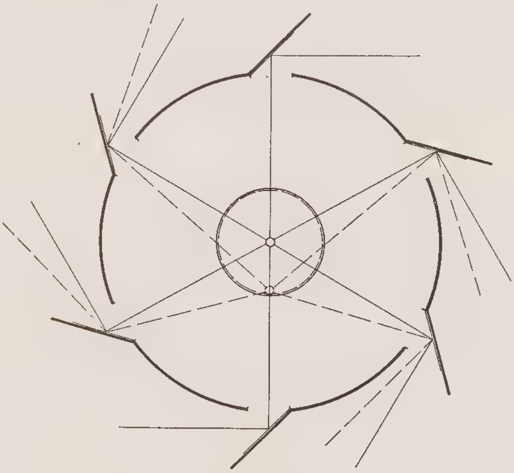


Fig. 5. Schema zur Veranschaulichung der Änderung der Reflexionswinkel bei exzentrischem Aufenthalt des Versuchsvogels.

(Fig. 4) kommen häufig vor, sind aber zwanglos zu erklären: 1. dadurch, dass der Star zwischen 6 diskontinuierliche Teilgesichtsfelder zu wählen hat, welche die Kontinuität seiner Windrose stören; 2. dadurch, dass der Star sich häufig nicht im Zentrum, sondern bevorzugt an einer Seite des Versuchskäfigs aufhält. Dadurch werden die Winkel, unter denen die einfallenden Strahlen am Spiegel reflektiert werden, stark verändert (Fig. 5).

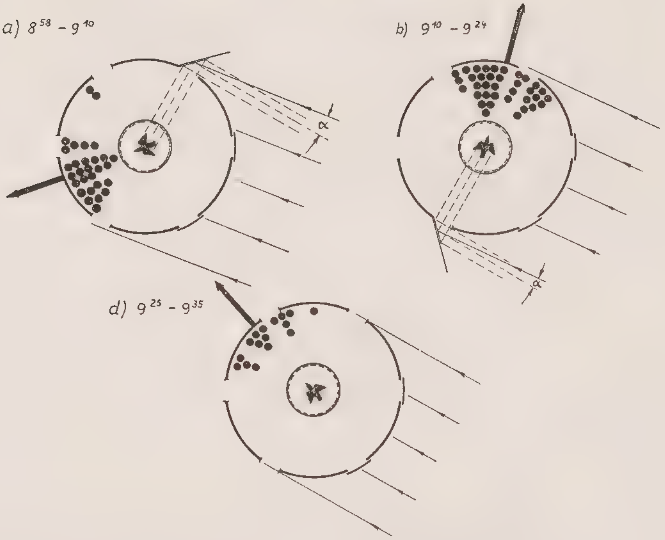


Fig. 6. 1-Spiegel-Versuch: Durch ein einziges Fenster wird gespiegeltes sonnennahes Himmelslicht auf den Vogel geleitet. Die Sicht sonstiger sonnennaher Himmelsausschnitte ist durch Schliessen der betreffenden Fenster verhindert. Der sonnennahe Himmelsausschnitt siegt ob über die 3 anderen sichtbaren Himmelsausschnitte, bewirkt aber Ablenkungen von weniger als 90°. — α = „Sonnenwinkel" (siehe Text).

Beim Herumprobieren machten wir bald eine wichtige weitere Entdekkung: Sonnennahes Himmelslicht wirkt stärker als sonnen-abgewandtes Himmelslicht. Dies wurde dadurch erwiesen, dass ein einziger Spiegel zu 3 anderen Gesichtsfeldern in Konkurrenz gesetzt wurde (Fig. 6). Man ersieht aus der Abbildung, dass 2 Fenster abgeblendet wurden — notwendigerweise, um das Eindringen von anderem sonnennahen Licht oder gar von direktem Sonnenlicht zu verhindern. Ein einziger sonnennaher Himmelsausschnitt, dessen Licht durch einen Spiegel auf den Versuchskäfig geleitet wurde, bewirkt eine Ablenkung der Richtungstendenz des Vogels, allerdings meist nicht um 90° von seiner Grundrichtung, sondern um weniger: Im abgebildeten Fall um etwa 60° im einen sowie im anderen Sinne.

Aus dieser Fig. 6 erkennen Sie auch das, was wir in unserer Laborsprache als den Sonnenwinkel bezeichnen: Nämlich den Winkel, welcher von der Einfallsrichtung der Sonnenstrahlen einerseits und vom Mittelstrahl eines gespiegelten Gesichtsfeldes andererseits eingeschlossen wird. Auf der Figur ist dieser Winkel sehr klein; er kann aber auch grösser sein, jedoch hat er nach unseren bisherigen Ergebnissen eine wohldefinierte Grenze, die

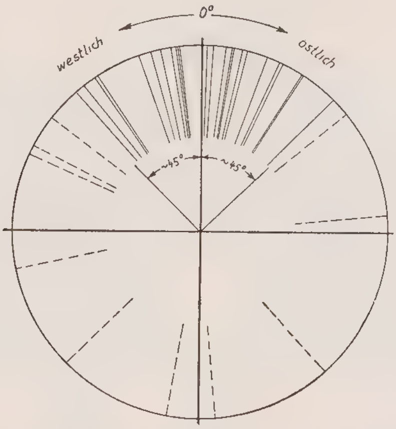


Fig. 7. Aus einem Bereich von 45° jederseits der Sonne (= 0°) kommt Licht mit orientierender Wirkung. Jeder der auf die Kreisperipherie auftreffenden Striche gibt den Sonnenwinkel eines Versuches wider. Ausgezogene Striche: Ablenkungseffekt; unterbrochene Linien: Kein Ablenkungseffekt.

aus Fig. 7 hervorgeht: Etwa 45°. Daraus geht unter anderem klar hervor, dass nicht (oder nicht nur) das direkte Sonnenlicht diese übermächtige Steuerwirkung hat, sondern auch Himmelslicht aus der Nähe der Sonne. Schon daraus geht hervor, dass der Vogel grundsätzlich die Fähigkeit hat, die Sonne auch nach indirekten Merkmalen zu lokalisieren. Wir wissen noch nicht, ob er sich dabei nach quantitativen Merkmalen (Intensität) oder etwa nach der qualitativen Verschiedenartigkeit des sonnennahen Himmelslichtes richtet, das ja reicher an langwelligen Anteilen ist als das sonnenfernere, blauere Himmelslicht.

Die Ergebnisse, die ich hier mitteile, sind völlig frisch, nämlich in diesem Frühjahr gewonnen. Wir konnten in dieser Periode noch keine Klarheit über die wichtige Frage erlangen, ob der Vogel auch imstande ist, seine Richtung dann zu finden, wenn wir ihm jegliches sonnennahes Licht nehmen. Was wir bis jetzt getan haben — z. B. im 1-Spiegelversuch —, beweist ja nur, dass sonnennahes Licht in Konkurrenz mit sonnenabgewandtem Licht obsiegt. Die erdrückende Übermächtigkeit, die sich in unseren Versuchen kundtat, mag mit unseren besonderen Versuchsbedingungen zusammenhängen. Vielleicht braucht der Vogel grössere sonnenferne Himmelsflächen, als die in unserem Versuchspavillon dargebotenen, um nach ihnen den Sonnenstand zu lokalisieren. Wir hoffen im Herbst darüber Klarheit zu gewinnen.

Ich weise vor allem darauf hin, dass Versuche mit allseitiger Spiegel-

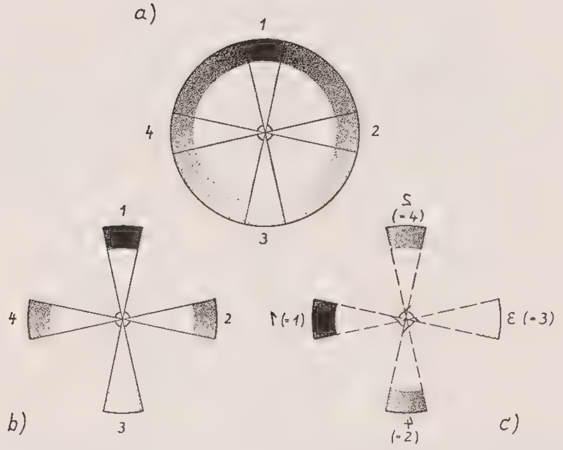


Fig. 8. Schema der Spiegelwirkung, der Einfachheit halber für den Fall von 4 Spiegeln. a): Der horizontnahe Himmel ist durch einen Ring mit bilateralsymmetrischen Helligkeitsgefälle wiedergegeben. Die Stelle des Sonnenvertikals mag in 1 oder 3 liegen. — b): Die 4 Teilgesichtsfelder sind isoliert. — c): Der Spiegeleffekt (Spiegelstellung A), wie er dem Star erscheint. Jedes der 4 Teilgesichtsfelder rückt um 90° im Gegen-Uhrzeigersinn herum. Die Reihenfolge der Teilgesichtsfelder bleibt erhalten. Jedes der Teilgesichtsfelder ist aber in sich um 180° verkehrt, sodass die Struktur mit der Reihenfolge nicht mehr harmoniert. (Nur je 2 gegenüberliegende Teilgesichtsfelder harmonieren miteinander.)

anordnung keine Auskunft geben können über eine Fähigkeit des Vogels, sich nach einer Struktur der ihm sichtbaren Himmelsausschnitte zu orientieren, also beispielsweise nach der Polarisation ihres Lichtes. *Strukturelle* Eigenschaften des einzelnen Teilgesichtsfeldes werden spiegelbildlich verkehrt wiedergegeben, aber die Struktur harmoniert nicht mehr mit der *Aufeinanderfolge*. Der Vogel muss darauf verzichten, sich im Spiegelversuch nach ihnen zu orientieren, auch wenn er es ohne Spiegel kann. Die nähere Erläuterung zu dem eben Gesagten gibt Fig. 8.

Ich habe bisher so getan, als ob der Himmel immer heiter wäre. Der Feldornithologe weiss aber, dass auch bei bedecktem Himmel gerichteter Vogelzug zu beobachten ist. In der Tat war die Richtungstendenz unseres Versuchsstars auch bei erheblicher Bewölkung gerichtet; jedoch nicht unbegrenzt! Fig. 9 a zeigt die längste registrierte Periode ungerichteter Zugaktivität bei sehr homogen und dunkel verhangenem Himmel. Um die Mittagszeit des gleichen Tages zerriss die Bewölkung, der Star nahm seine gewohnte Richtung auf, und wir erhielten das Diagramm 9 b.

Man kann die Streuung des Lichtes auch durch eine Art künstlicher Nebelschicht herbeiführen, indem man nämlich Pergamentpapier vor die Fen-

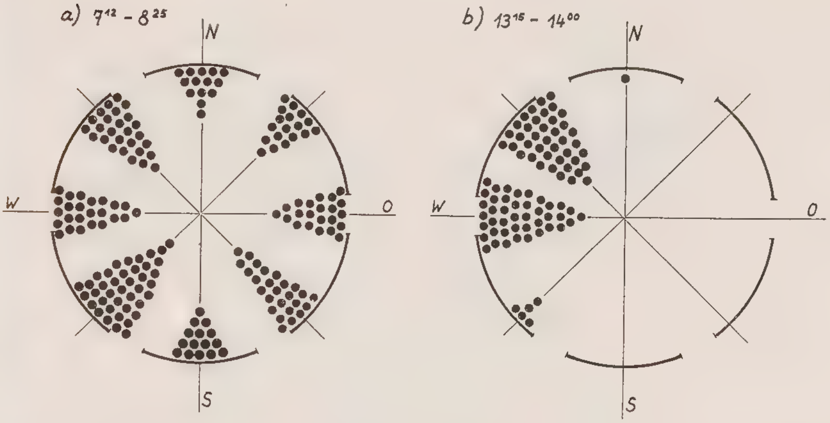


Fig. 9. Richtungsdiagramm bei sehr dunkler Bewölkung (a) und bei darauffolgender Aufheiterung (b).

ster setzt. Der Star bleibt gerichtet und kann durch Spiegel abgelenkt werden, wie Fig. 10 zeigt.

Zum Schluss möchte ich Sie noch mit einer Erscheinung vertraut machen, die mir für das Verständnis mancher Schwierigkeiten, denen der ziehende Vogel begegnet, von grösster Bedeutung zu sein scheint, nämlich mit der Beharrungstendenz. Als ich den allerersten Versuch mit allseitig vorgesetzten Spiegeln unternahm, war das Ergebnis eine deutliche Störung, die aber kein quantitativ befriedigendes Bild gab. Daraufhin tapezierten wir die Innenwände des Pavillons homogen aus und erhielten sofort einen klaren Ablenkungserfolg. Schon dadurch wurde klar, dass der Vogel sich nicht nur von Himmelsmerkmalen, sondern zusätzlich auch durch Nahmerkmale lenken liess. Fern- und Nahmerkmale werden ja im Spiegelversuch auseinandergerissen, während sie in der Natur miteinander harmonieren. Aus Fig. 10 b ersehen Sie, in welcher Form sich ein Beharrungseffekt ganz regelmässig manifestiert: Dadurch, dass der Vogel sich nur langsam von seiner Grundrichtung ablöst, und zwar in diesem Fall vermutlich durch die Wirkung kinästetischer Merkmale.

Sehr drastisch kommt der Beharrungseffekt in Fig. 11 zum Ausdruck, wo dem Vogel zunächst eine Richtung aufgezwungen wurde, die von seiner Grundrichtung um etwa 90° abweicht. Nach Wegnahme der Blenden auf der sonnenabgewandten Seite hält er an der ihm aufgezwungenen Richtung fest, und erst wie wir ihm sonnennahes Licht zur Verfügung stellen, findet er sich wieder.

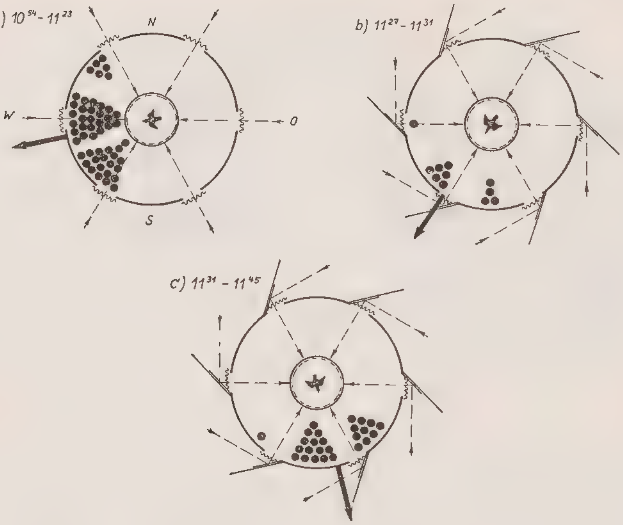


Fig. 10. Ablenkungseffekt bei Vorschaltung von Pergamentpapier. a): Grundrichtung SSW (vgl. Text). — b): Zwischenperiode unmittelbar nach Vorsetzen der Spiegel; die Ablenkung ist noch keine vollständige. — c): Ablenkung um 90°.

Zweifellos haben wir es hier mit einer äusserst nützlichen Einrichtung zu tun, welche es dem Vogel ermöglicht, Perioden, in denen ihm die Originalmerkmale nicht zugänglich sind, zu überbrücken. Meist werden die Überbrückungsmerkmale optischer Art sein, wobei das Landschaftsbild in unseren Versuchen durch die Innenwände des Turmes vertreten wird. Es ist aber nicht auszuschliessen, dass ein Vogel ohne Windstörung auch auf Grund kinästhetischer Daten eine kürzere Strecke geradlinig zurücklegt, aber die Fehler würden wohl in kurzer Zeit das Mass des Erträglichen überschreiten.

Zum Schluss noch einige Worte über die Bedeutung, die ich für unsere Wilhelmshavener Versuche fordere. Es ist danach in einem speziellen Fall der Nachweis geführt, dass ein Vogel imstande ist, sich allein nach optischen Himmelsmerkmalen zu orientieren. Es gibt nur ein einziges Zentrum, das dem Tageshimmel eine gesetzmässige Struktur verleiht, das ist die Sonne. Unsere Versuche haben bisher nur erwiesen, dass der Star sich nach der groben optischen Struktur des Himmels richtet. Wir vergessen nicht, dass es auch denkbar ist, dass feinere Strukturbestandteile benutzt werden, die dem Vogel gestatten würden, schon aus einem der 6 Teilgesichtsfelder den Stand der Sonne zu erschliessen; wir müssen dabei hauptsächlich

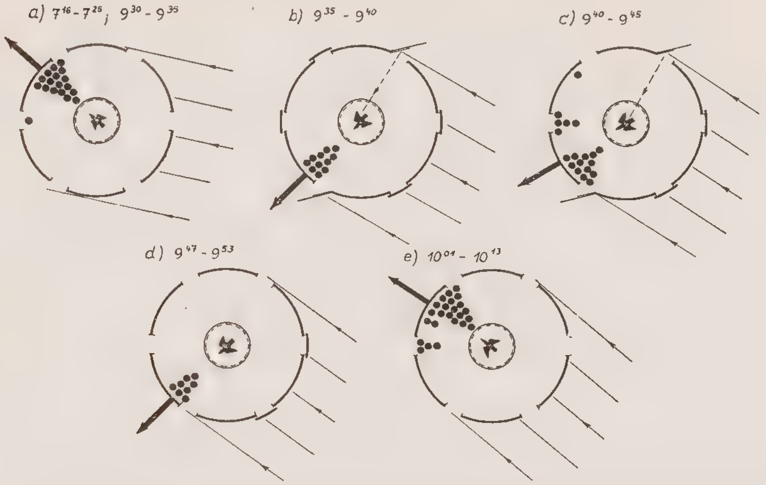


Fig. 11. a): Grundrichtung; b): dem Vogel wird eine bestimmte Richtung aufgezwungen; c) und d): Er beharrt auf dieser Richtung, auch nachdem Verschlüsse und Spiegel entfernt sind; e): Zutritt von sonnenseitigem Licht stellt die Grundrichtung wieder her

an die Polarisation des Himmelslichtes denken, die ja von der Biene wahrgenommen und zur Ortung der Sonne benutzt wird (v. Frisch). Wie schon auseinandergesetzt wurde, sind unsere bisherigen Versuche nicht geeignet, Aussagen über eine derartige Fähigkeit bei Vögeln zu machen. Der wesentliche Punkt ist der, dass die Sonne als das steuernde Zentrum erkannt wurde. Auf welche Weise die nicht direkt sichtbare Sonne geortet wird, werden hoffentlich unsere weiteren Studien zeigen. Ich wage die Voraussage, dass der Vogel über mehrere Methoden verfügt, die er kombiniert in Anwendung bringt.

Es ist sicher, dass der Vogel die von ihm einzuhaltende Richtung errechnen muss. Unsere Versuche erstrecken sich über eine Spanne des Tages, in der die Sonne einen Winkel von 90° zurücklegt. Die Richtung unseres Vogels bleibt meist innerhalb der Grenzen der Ablesungsgenauigkeit die gleiche, manchmal schwankt sie um etwa 30°. Der tatsächliche Stand der Sonne in jedem Augenblick ist nur eines der 3 Daten die hierzu nötig sind. Die zweite Grösse ist die Tageszeit, die offenbar in der zentralen Rechenmaschine mit grosser Präzision fortgesetzt dargestellt wird. Und die dritte ist die Winkelgeschwindigkeit, mit der die Sonne sich über den Himmel bewegt. — Es ist unser Ziel, alle 3 Komponenten, welche zur Errechnung der innezuhaltenden Richtung notwendig sind, möglichst deutlich in Evidenz zu bringen.

## Summary

Captive starlings (*Sturnus vulgaris* L.) show marked directional tendencies during their migratory activity. In the autumnal migration period these trends are in agreement with the natural direction of migration. — In spring "good" directions were held during a period of 10 days only; northwest activity being recorded during the following period. This constant northwest tendency was used as a basis for experiments with the aim of modifying the direction maintained by the bird.

The visual range of the latter was reduced to six equally distributed openings which permitted a view of sky cuts slightly above the horizon. No view of land marks was allowed (see Figs. 1, 2).

If mirrors are put before each of the 6 windows in such a manner as to deflect the direction of the incidental light at an angle of 90°, the bird will change its direction according to this deflection (Fig. 3, 4.) It has been proved that light which originates in the proximity of the sun plays a predominant part as a stimulus for orientation. (Fig. 6.)

Orientation and, consequently, its experimental modification will work under a bright sky, but also under a cloud covering up to a certain degree of compactness. If the sky covering becomes too heavy the migratory activity becomes haphazard. (Fig. 9.) Artificial diffusion of light by semitransparent paper (vellum type) does not check, but weakens orientation. (Fig. 10.)

There is a marked tendency to perseverance which, in the case of experimental deviation of the incidental sky light, may interact with sky orientation. The basis of what is called perseverance is supplied by the close visual surroundings of the bird, i. e. the inside of the experimental pavilion. Purely kinaesthetic perseverance cannot be ruled out. Close sight marks are thought to replace landmarks under natural conditions.

It is emphasized that the particular conditions of the mirror experiment did not allow the bird to manifest faculties beyond those demonstrated. More detailed properties of the sky (e. g. polarization) could potentially enable the bird to localize the sun on the basis of structural qualities of small parts even of sky regions opposite to the sun; but in changing the incidence angle of the sky light by 90° the structural features within each of the visible sky parties get additionally inverted by 180°, thus causing conflicting experimental effects. (Fig. 8.)

It is stressed that, in our case, the ultimate source of orientation is the sun, with whatever methods of spotting it the bird may be endowed. The ability to appreciate daytime and an elaborate faculty of computing the "desired" direction on the basis of: actual sun position; daytime; angle-speed of the sun movement, must consequently be assumed.

# Some notable factors concerning the migration of palaearctic birds

*Gustaf Rudebeck*

*Zoological Institute, Lund, Sweden*

The migratory behaviour in birds shows a very great variation and manifests itself to a very varying extent. Some species show extremely elaborate migratory habits, other species less so, others still are only partly migratory or irregular migrants, and finally many species are resident and sedentary, although in many cases indications of migratory behaviour can be seen. Within every species, different populations very often differ widely as to their migratory habits. On the other hand, neighbouring populations usually show considerable overlap in this respect.

Terrestrial birds breeding in the western and central parts of the palaearctic region show a striking parallelism concerning their migratory habits. Of course there are some exceptions, but, in the great majority of cases, within every species the western and southern populations are migratory to a lesser extent than are the populations breeding in northern and eastern areas. This is true, whether we judge from the percentage of specimens which emigrate, or from the regularity with which the migration is performed, or from the distance traversed from the breeding grounds to the area of hibernation. The variation is in the form of a cline, the steepest gradient being from WSW to ENE, but of course the cline is not equally steep for every species, neither is it equally steep all the way. Some species, e.g. *Pica pica* and *Perdix perdix*, are resident in the main part of Europe and more or less migratory only in the north-eastern parts of the continent. Many other species are resident in western Europe but clearly migratory in central Europe and further eastwards. Still other species are migratory all over their breeding range, but the distance between breeding area and winter quarters is much longer in the case of the eastern populations.

In a very large number of species the main direction of migration also forms a cline. If the westernmost populations migrate at all, they usually move approximately southwards. Birds from Scandinavia and central

Europe as a rule migrate in a southwesterly direction, and birds from northeastern Europe and western Siberia move ENE—WSW or even due E—W. In other words, the migratory directions converge against western and southwestern Europe and adjacent parts of Africa. Most species hibernate here, but some proceed further southwards into the tropics.

As is well known, a limited number of species migrate approximately towards the southeast from their European breeding places. In these cases the main directions of migration converge towards southeastern Europe, Asia Minor, and Egypt. Out of the birds belonging to this group, most species move further south and hibernate in tropical or south Africa.

There is an obvious correlation between the migratory habits of the SW-migrants and the climatic conditions in the area, in which they breed, but as a whole this group shows a great deal of individual variation as to their migratory habits. Among the SE-migrants this variation is not at all so pronounced, their migratory habits being much more elaborate and fixed and the distance between breeding area and winter quarters very considerable. Many species, which have spread over Europe from the east and southeast, belong to the SE-migrants (*Oriolus oriolus, Coracias garrulus*, several warblers and buntings, etc.).

A feature, which complicates the picture given above, is the occurrence in many species of a "migratory divide" (called "Zugscheide" by German authors). In each of these species, the birds breeding to the west of this zone migrate towards the southwest, the birds breeding to the east of it leave in a southeasterly direction. The phenomenon is particularly well known in *Ciconia ciconia*, but also in *Motacilla alba* and several others. The geographical position of the migratory divide is different in different species. Sometimes the occurrence of this zone can possibly be explained from the postglacial history of the species, but certainly this is not always the case. Many SE-migrants seem to possess a peculiar disposition towards the development of such a migratory divide, or rather an "unstable zone", in their westernmost breeding areas (*Muscicapa parva, Anthus cervinus*, etc.). The writer is inclined to believe that many records of rare vagrants in western Europe can be explained from this assumption, the interpretations of these records as birds which have gone astray being less satisfactory. The possibility cannot be excluded, that some common factor, releasing this migration towards the southwest, is at work. It should be kept in mind, too, that *if* migratory movements are observed in so-called resident birds, these movements in most cases are directed towards the southwest in northern and central Europe.

This communication, as well as my earlier discussion of the subject

(Rudebeck 1950, p. 55—68 and 72—75), necessarily have a preliminary character. The problems involved are very complicated and should be considered in relation to the orientation of migratory birds, the occurrence in certain species of different routes during spring and autumn migration, changes in distribution and migratory behaviour, the influence of one bird upon another by induction, modern taxonomic work, field studies in certain areas, etc. On the other hand, the accumulated knowledge concerning these questions should now make it possible to perform a synthetical work of this kind.

*Discussion:*

A. Landsborough Thomson suggested that it would be very valuable if ornithologists having the opportunity would make an intensive study of a »Zugscheide» such as had been mentioned, using ringing and other methods. One would like to know how the line runs and how exactly it is drawn in nature. Is it a sharp division, so that birds living a short distance apart must migrate quite differently? Or is there a transitional belt of some breadth; and, if so, what determines the migration direction of individual birds within it? Satisfactory data on such points would be of much theoretical interest.

R. Drost: Der Unterschied, ob Zugvogel, Strichvogel oder Standvogel, zeigt sich nicht nur bei verschiedenen Arten und Populationen, sondern er tritt sogar in derselben Familie auf, wofür Beispiele aus der Vogelberingung vorliegen, z. B.: von 2 Nestgeschwistern von *Turdus merula* überwinterte einer in der Heimat bei Frankfurt/Main, während der andere nach Sydwestfrankreich zog.

## Reference

Rudebeck, G. 1950: Studies on bird migration, based on field studies in southern Sweden. Vår Fågelvärld, Suppl. 1. Lund.

# The Relation of Spring Migration to Day Length and Solar Radiation

*Axel M. Hemmingsen*

*Copenhagen*

Fig. 1 shows how day length and culmination height of the sun varies throughout the year at the various latitudes of the northern hemisphere, and also shows the northward movement of the vanguards of various American, European, and Asiatic migrating bird species in spring, through their breeding ranges. The dotted lines in spring show movements before the breeding range is reached. The autumn movements of a few species have been introduced for comparison. The dotted lines in autumn are, however, queried and of a tentative character.

The well known fact, that the later a species migrates in spring the faster it moves, is thus illustrated by the rising steepness of the bird lines with advancing spring; and the rise in speed with rising latitude, by an upward curve.

A few of the earlier species may be "weather" birds, but the majority are "instinct" birds.

A number of species other than those represented in fig. 1, have also been included in the considerations to follow. Their inclusion in fig. 1 would have produced too much coinciding of the lines. For species with both Atlantic and Continental migration routes more than one line can be drawn; and in the considerations to follow, such species have been represented by two lines corresponding to two extreme routes.

It is quite remarkable that the reference of speeds to latitude leads to nearly identical speeds for some species that differ up to 100 per cent in actual speeds in terms of km per unit time (broken line 1 representing (22) both *Lanius collurio, Muscicapa striata* and *Oriolus oriolus*) and brings a line like that of *Emberiza melanocephala* (line L) into the radial system of others that migrate towards N or NE, though this species migrates towards WNW-NW.

The tendency towards a regular radial arrangement of the bird lines

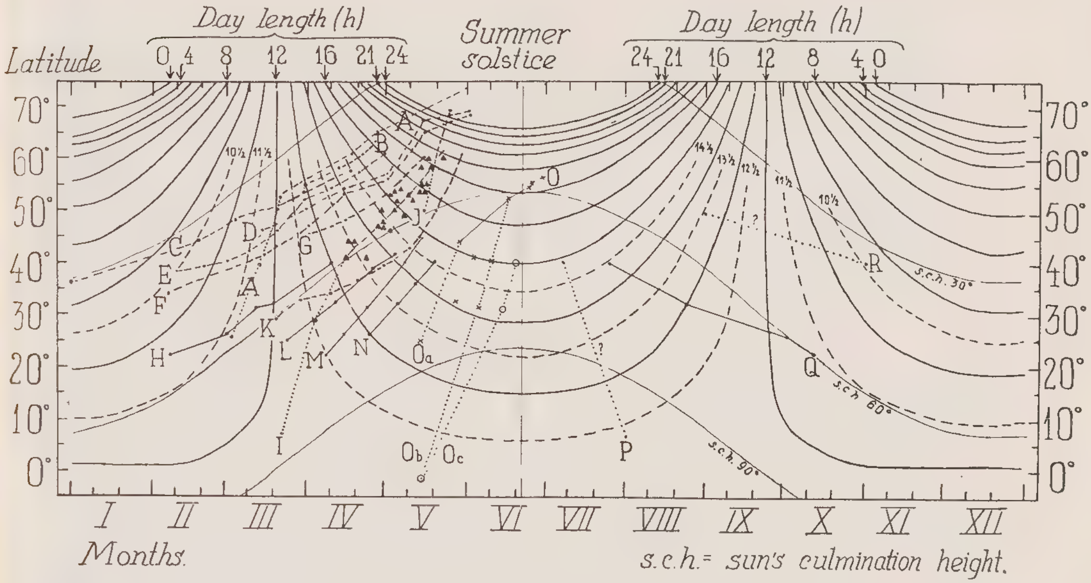


Fig. 1. The migration speeds of the vanguards of various species in relation to the changes in the sun's culmination height and in day length with latitude and advancing seasons.

By means of the curved whole lines at the upper ends of which day lengths are given in hours (h), together with the intermediate curved broken lines at the upper ends of which the day lengths are given for the intermediate half hours, the length of day prevailing at any of the latitudes (ordinates) on any given date (abscissae) can be found.

The other lines in the figure, which are for the most part more or less perpendicular to the day length lines, show to which latitude in spring (ordinates) the vanguards of the different species (A– O)have penetrated on any given date (abscissae) during their journey towards the North. The day lengths, which prevail at the different times at the different latitudes which the vanguards pass during these movements, can be read from the day length lines which the "bird lines" cut or from interpolations between the day length lines. The few (three) bird lines in autumn illustrate in the same way the latitudes (and the day lengths prevailing there) to which the vanguards of these birds have penetrated during their southward journey through areas in which they do not breed.

In the following lines figures in brackets refer to the list of references. My own observations are included as regards species occurring in North Eastern China.

East Asia, whole lines: H *Hirundo rustica gutturalis* (10), M *Oriolus chinensis diffusus* (10), N *Terpsiphone paradisi incei* (10), O *Locustella fasciolata*: Oa earliest arrival dates, Ob end points correspond to assumption of Stresemann (18, p. 680), Oc last dates (for references, see crosses underneath), Q *Emberiza aureola* (10); dotted lines in autumn: P *Tringa hypoleucos* (own obs.), R *Ciconia c. boyciana* (12). India—South-East Europe, whole line: L *Emberiza melanocephala* (21). Europe, broken lines: A *Oenanthe oenanthe* (22), B *Grus g. grus* (11), C *Ciconia c. ciconia* (13, 20), D *Phylloscopus t. trochilus* (15), F *Hirundo r. rustica* (14), G *Phylloscopus sibilatrix* (16), I *Lanius collurio* (19, 22). North America, broken lines: E *Branta canadensis* (3), J *Hylocichla aliciæ* (3), K *Vireosylva olivacea* (3). Triangles: Mean arrival dates of *Lanius collurio* (19, 22).

relative to the day length lines suggests a closer relationship between northward movement and day length.

The starting point of this study was the fact that the vanguards of the species migrating through China all gained 1 $^1/_2$ hours in day length from 22° N to 40° N in spite of their widely differing speeds.

If, now, the logarithms of the day length gains experienced between 20°–30° N, 30°–40° N, 40°–50° N, and 50°–60° N, by the vanguards of all the species studied within their breeding ranges, are plotted against the means of these ranges of latitudes, i.e. 25°, 35°, 45°, and 55° N, a regular linear relation results, the average day length gain rising with increasing latitudes, and varying, within each of the 10°–latitude ranges mentioned, with a standard deviation of only up to 20–25 per cent of the mean day length gain within each range.

This regular linear relation expresses mathematically the above-mentioned facts that speed increases with advancing spring and with rising latitude, for if the lines in fig. 1, which represent low speeds in the beginning of spring or at lower latitudes, are placed at the end of spring or at higher latitudes, or if lines representing high speeds at the end of spring and high latitudes are placed at the beginning of spring or at low latitudes, they fall far below or above the linear trend in question.

It is well known that most species, except the earliest ones, tend to move northwards at a higher speed than the isotherms. In accordance with this we find that if lines representing the northward travel in spring of various isotherms, are introduced in fig. 1 and their day length gains plotted against latitudes in the same way as just mentioned for the bird lines, they are less steep in fig. 1 than the bird lines. Also, their day length gains, when plotted against latitudes, do not show the regular linear relation just described.

But if the northward travels of different amounts of radiation received from the sun in terms of calories per unit of surface and time, as constructed from available tables, are drawn in fig. 1 as if they were birds migrating towards the North, a similar regular linear relation between day length gain and latitudes is obtained as with the birds.

It thus appears to me strongly indicated that there is an intimate relation between northward spring movements and solar radiation and the present

---

Line I represents an average of these triangles. Crosses: Arrival dates of *Locustella fasciolata* (1, 2, 8, 9, 10, 17, 18, 24, 25). Dotted lines in spring represent speeds south of the breeding ranges, broken and whole lines speeds within the breeding ranges.

To avoid too much coinciding and intersections of lines, the lines of the eastern European (more steep) and eastern American (less steep) routes have been omitted, except for *Lanius collurio* for which all European dates are covered.

study is to some extent a confirmation of views expressed earlier, for instance by Eckardt (4, 5) and Ekman (6). But on the other hand there are many points that invite discussion in detail.

It is, for instance, a question whether a direct response to the seasonal changes in radiation is involved or only an adaptation to them.

More details and relevant diagrams will be published in "Observations on Birds in North Eastern China. I. General Part. Spolia Zoologica Musei Hauniensis XI," published by the Zoological Museum of Copenhagen University.

## References

1. Austin, O. L. (1948). The Birds of Korea. Bull. Mus. Comp. Zool. Harvard, 101, 1–301, with 1 plate.
2. Cherski, A. J. (1915). Ornitologicheskie sbory v doline verkhnego techenia reki Odarki, Primorskoi obl. (Ornithological collections in the upper valley of the river Odarka, Primorski Gov.) Zapiski Obshchestva Isucheniya Amurskago Kraya (= Communications from the Association for investigations of the Amur country), 14, 79–141. Vladivostok. (Russian.)
3. Cooke, W. W. (1915). Bird Migration. Bull. U. S. Dep. Agric., No 185, 1–47.
4. Eckardt, W. R. (1910). Vogelzug und Vogelschutz. — Aus Natur und Geisteswelt, Leipzig.
5. —— (1918). Über die Entstehung des Zuges der Wandervögel. Die Naturwissenschaften, 6, Heft 42.
6. Ekman, S. (1922). Djurvärldens Utbredningshistoria på Skandinaviska Halvön (The history of distribution of the animal world in the Scandinavian peninsula). Stockholm. (Swedish.)
7. Hartert, E. and Mayr, E. (1930). On a collection of birds made by Dr. Ernst Mayr in northern Dutch New Guinea. Novitates Zoologicae, 36, 18–128.
8. Johansen, Hans (1935). Die Brutvögel des Salairgebirges. Trudy Biol. Inst. Tomsk Universit. No. 1, 12–65 Tomsk. (Russian with short summary in German.)
9. La Touche, J. D. D. (1906). Field Notes on the Birds of Chinkiang. Lower Yangtse Basin, Part I. Ibis, London, 6, 427–450 and continuation.
10. —— (1925–34). A Handbook of the Birds of Eastern China, Vol. I–II, London.
11. Middendorff, A. v. (1855). Die Isopiptesen Russlands. Mém. Acad. Sci. St. Pétersb., VI Sèr., Sci. nat. 8. Reprint (with two maps) of paper not published until 1859 (without maps, at least in the Copenhagen Univ. Library copy).
12. Schrenck, L. v. (1860). Reisen und Forschungen im Amur-Lande, Band 1, 2. Lieferung, Vögel des Amur-Landes. St. Petersburg.
13. Sliwinsky, Ursula (1938). Isopiptesen einiger Vogelarten in Europa. Zoologica Poloniae, 2 (1937–38), 249-287 (with 5 plates).
14. Southern, H. N. (1938 a). The Spring Migration of the Swallow over Europe. Brit. Birds, 32, 4–7.
15. —— (1938 b). The Spring Migration of the Willow-Warbler over Europe. Brit. Birds, 32, 202–206.
16. —— (1940). The Spring Migration of the Wood-Warbler over Europe. Brit. Birds, 34, 74–79.

17. Stegmann, B. (1930–31). Die Vögel des dauro-mandschurischen Übergangsgebietes. J. Orn., 78, 389–471, with a map and a plate, 79, 137–236.

18. Stresemann, E. (1927–34). Handbuch der Zoologie. Aves. Vol. 7, Hälfte 2.

19. —— (1944 a). Der zeitliche Ablauf des Frühjahrszuges beim Neuntöter (*Lanius collurio*). Orn. Monatsber., 52, 1–8.

20. —— (1944 b). Der Frühjahrsdurchzug einiger Vogelarten durch die Mittelmeerländer. Orn. Monatsber., 52, 29–44.

21. —— (1944 c). Der zeitliche Ablauf des Frühjahrszuges beim Kappenammer, *Emberiza melanocephala*, Scop. Orn. Monatsber., 52, 85–92.

22. —— (1948 a). Die mittlere Erstankunft von *Lanius collurio, Muscicapa striata, Oriolus oriolus* und *Oenanthe oenanthe* im europäischen Brutraum. Vår Fågelvärld, 7, 1–18.

23. —— (1948 b). Die Wanderungen des Pirols (*Oriolus o. oriolus*). Ornithologische Berichte, Mai 1948, p. 126–142. Heidelberg: Karl Winther.

24. Swinhoe, R. (1863). Catalogue of the Birds of China, with remarks principally on their geographical distribution. Proc. Zool. Soc. London, p. 259–339.

25. Taczanowski, Wl. (1893). Faune Ornithologique de la Sibérie Orientale. Mém. Ac. Sci. St. Pétersb., Sér. VII, 39, parts 1–2.

# The Relation of Bird Migration in North Eastern China to Body Weight and its Bearing on Bergmann's Rule

*Axel M. Hemmingsen*

*Copenhagen*

Fig. 1 shows the relation of body weight of bird species migrating to or through the area of Peitaiho Beach at the coast of North Eastern China, to the first date they have been observed in spring. It will be seen that the later the spring arrival, the smaller is the average body weight. In autumn, inversely, the later the departure, the greater is the average body weight. The fall in body weight during spring and the rise during autumn are statistically highly significant.

Now, what is the explanation of this? It might be suggested that larger birds need longer time at their breeding grounds for their young to grow up than small birds. But on the other hand small birds tend to have more than one brood. There are also many examples of adults that remain in the breeding area long after the young have left. In other groups the adults leave before the young. The data available on brood numbers are too few for the East Asiatic birds for a statistical test of this explanation to be made.

Another explanation is that we are concerned with a special aspect of Bergmann's rule according to which great body size is associated with greater resistance to cold than small body size. As a matter of fact about one century ago Bergmann (1) gave a number of examples showing that in Europe large migrants travelled at colder periods than smaller migrants.

If this were the explanation, we should expect the early migrants to breed and winter in colder areas than the smaller ones.

In some groups of species (e.g. flycatchers and ducks) this is actually the case.

In some other groups (e.g. the *Emberiza* species and the *Turdidae*) the breeding areas of the later spring migrants are not significantly more northern than those of the early ones. But on the average the later migrants will, of course, arrive in the breeding areas at a higher temperature than the early migrants.

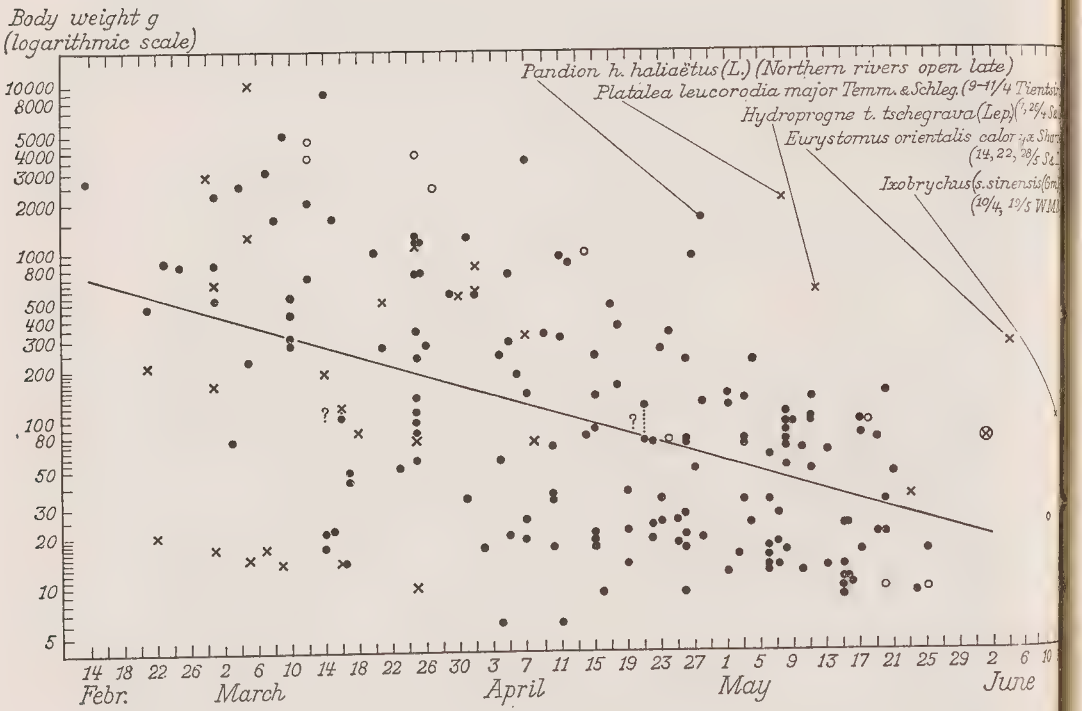


Fig. 1. The relation of body weight of spring migrants at Pei-tai-ho Beach to first date of observation in spring.

Each open or filled circle or cross represents one particular species.

The crosses must be taken with some reservation because the species they represent may occur a good deal earlier, in some of the cases even in winter.

The body weights (almost always of males) are from T. H. Shaw (13) except a few which are either from Groebbels, Kirchner and Moebert (5) or have been assessed with approximation (marked as open circles) from the known body weights of related forms of similar size, assuming the body weight to be approximately proportional to the third power of the linear measures. In some cases body weights from Weigold (16) have been utilized for this. The uncertainty involved in this is, of course, negligible compared with the dispersion of the body weights of all the birds arriving at the particular time.

The earlier arrival of some species in other parts of North China (Hopei Province), as given in the upper right corner of the figure, would bring the odd points representing these species in the figure nearer to the bulk of points. S&L means Seys and Licent (12); WMN, Wilder's Migration Notes (17, p. 397, and 18, p. 135).

In all such cases as those mentioned, the later spring migrants winter farthest to the South. So as far as may be seen from all this, Bergmann's rule might well be the explanation; i.e. a higher degree of thermophily might be postulated for the later and smaller migrants compared with the earlier and larger ones.

Not only when all the species are treated collectively as in fig. 1, but also when some groups of related species are selected, the fall in body weight during spring migration can be shown to be statistically significant. This is true, for instance, as regards the ducks and also as regards the waders represented in fig. 2.

Now, fig. 2 shows that in contrast to the other groups mentioned, the waders that migrate latest have more northern breeding ranges than the earlier migrating waders, and they penetrate so far south in winter that they get to colder regions in the southern hemisphere than the earlier and on an average larger migrating waders. Both the average lines drawn in fig. 2 have been calculated by the method of the least sum of squares and their inclinations are highly significant statistically. I have ascertained that the extensions of known ranges of waders in New Zealand communicated to this Congress by Dr. R. B. Sibson, affect this picture only negligibly. I am grateful to Dr. Sibson for details given *in litt.*

The fact that later migrants tend to travel farthest south has been established earlier for some German birds (15, p. 703).

Not only do the small and late waders breed farthest to the North, they actually breed at lower temperatures. In their arctic breeding grounds, for instance, the mean temperature does not rise above 4°–5° C. This fact is also illustrated by the distribution of the two curlews *Numenius arquata* and *Numenius phœopus* in the Scandinavian peninsula. The former, which is the earlier and larger of the two, was found by Ekman (4) to be limited in its breeding range by the 9° C minimum temperature; the latter, by the 15° C maximum temperature.

In other words, in the waders the smaller and later species in spring are not the most heat-loving but apparently the most cold-loving, at least in the breeding season and at the high latitudes where in summer the day is long enough for them to eat enough.

It is rather striking that when the size is compared among related birds of species that are wintering or not wintering in certain areas, the wintering birds are found to be of greater size. There are a number of such examples in North Eastern China.

I have also compared the body weights of such waders, as are known to winter in Denmark (7) with the body weights of the rest of the waders

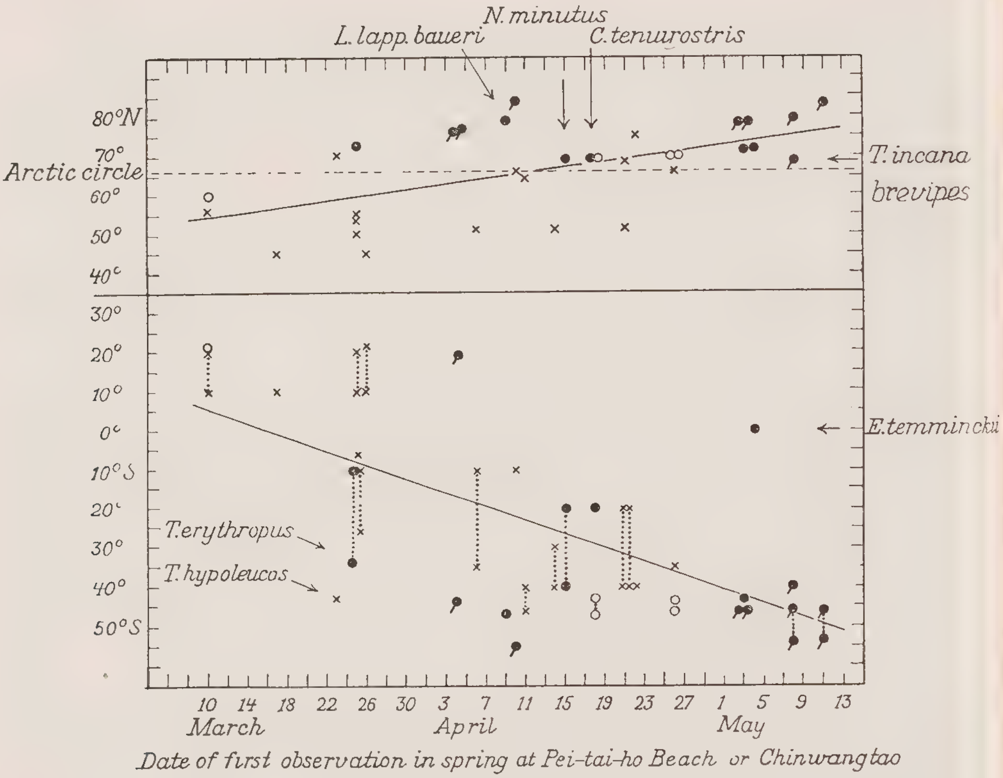


Fig. 2. The relation of northern limits of breeding and southern limits of winter ranges of waders (*Charadriidae* in Hartert's sense, yet excluding *Scolopacinae* sensu restricto) to dates of first observations in spring at Pei-tai-ho Beach.

Each species is represented by one point for the northern limit of the breeding range and by one point (or a pair of points connected by a dotted line) for the southern limit of the winter range.

The lowest of two points connected by a dotted line is the least reliable, sometimes basing only on rare occurrences of the respective species. The black discs with a mark at the bottom to the left represent the only species breeding, solely or partly, in the arctic tundra (11) or, in case of *Tringa incana brevipes* (Vieill.) (probably) in the alpine mountain region (14), the black discs without a mark represent typical subarctic, or, in the case of *Numenius minutus* Gould, subalpine breeding, and the open circles, partly subarctic breeding, according to information kindly given to me by Prof. Dr. Hans Johansen (with a particular view to Siberian conditions).

The north limits of the breeding ranges have been revised by Prof. Hans Johansen for Siberia, but more northern breeding occurrences in other parts of the world have been preferred, if on record in the sources of information consulted. Winter records from all continents have been allowed for. For polytypic species only the ranges of the subspecies passing Pei-tai-ho Beach have been considered.

The literary sources of the ranges are given under References (2, 3, 6, 8, 9, 10, 11, 13, 14, 15).

visiting Denmark, and I found that on a statistical average basis the former weigh significantly more than the latter.

One might be inclined to see in this a confirmation of Bergmann's rule. It is clear, however, that the larger ones may remain in an area in winter merely because the smaller ones are urged by their migratory instincts to penetrate further to the South than the larger ones, no matter whether this leads them to warmer or colder areas.

We do not understand, however, why there is such an association between on the one hand early spring migration, late autumn migration, large body size and northern winter quarters and on the other hand late spring migration, early autumn migration, small body size and southern (including southern hemisphere) winter quarters.

More details including relevant diagrams will appear in: "Observations on Birds in North Eastern China. I. General Part. Spolia Zoologica Musei Hauniensis XI," published by the Zoological Museum of Copenhagen University.

*Discussion:*

R. Meinertzhagen: I have weighed many thousands of migrating birds both during passage, at the commencement of passage and on arrival at breeding quarters. The following results are worthy of special note:

1) Females are heavier than males at spring passage.

2) Birds are at their heaviest during spring passage, rapidly losing weight on arrival at breeding stations.

3) Birds are at their lightest weight immediately before the autumn moult and during the first few days of that moult.

4) Usually, long distance spring migrants are fatter than those undertaking shorter flights.

A. M. Hemmingsen: The seasonal changes in body weight of any single migratory species, especially due to heavy deposition of fat at the beginning of migration and absent in non-migrating birds represent much smaller changes in body weight than the change in average weights of different species here concerned.

## References

1. Bergmann, C. (1847). Ueber die Verhältnisse der Warmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien. 1 Abt. (math. u. naturw. Abh.) II. Lieferung, 595-708. Göttingen.
2. Buller, W. L. (1888). A History of the Birds of New Zealand, Vol. II. 2nd edition. London.

3. Caldwell, H. R. and Caldwell, J. C. (1931). South China Birds. Shanghai: Vanderburgh.
4. Ekman, S. (1922). Djurvärldens Utbretningshistoria på Skandinaviska Halvön (The history of distribution of the animal world in the Scandinavian peninsula). Stockholm. (Swedish.)
5. Groebbels, F., Kirchner, H. and Moebert, F. (1938). Ornithologische Hilfstabellen. Berlin.
6. Hartert, E. (1903–1923). Die Vögel der paläarktischen Fauna. Vol. I–III (1910–1922) and Nachtrag I (1923). Berlin. Heft 1 appeared 1903; but Vol. 1, not until 1910. Ergänzungsband 1932–38, see Steinbacher.
7. Hørring, R. (1926). Fugle (Birds), II. Danmarks Fauna, 30, Copenhagen. (Danish).
8. La Touche, J. D. D. (1925–34). A Handbook of the Birds of Eastern China, Vol. I–II, London.
9. Mathews, G. M. (1910–1927). The Birds of Australia, London. Vol. III (1913–1914) and Supplement No. 1: Check list of the birds of Australia (1920–1924), Part I.
10. Niethammer, G. (1937–1942). Handbuch der deutschen Vogelkunde. Vol. I–III. Leipzig.
11. Pleske, T. (1928). Birds of the Eurasian Tundra. Mem. Boston Soc. nat. Hist., 6, No 3, 109–485.
12. Seys, G. and Licent, E. (1932–1934). La Collection d'oiseaux du Musée Hoang ho Pai ho de Tien Tsin. With loose green sheet with Liste d'Errata. Avril 1932. Additions, faites de 1928 à 1933 à la Collection, etc., Avril 1934. Editeurs: Mission de Sien Hsien, Race Course Road, Tientsin 1933. Publications du Musée Hoang ho Pai ho de Tientsin, No. 19 and 31.
13. Shaw, T. H. (1936). The Birds of Hopei Province, Vol. I–II. Fan Memorial Institute of Biology, Peiping (Peking). Zoologia Sinica, Ser. B, 15, Fascicle I.
14. Steinbacher, F. (1932–1938). Co-author with Hartert of supplement to Hartert: Die Vögel der paläarktischen Fauna. Ergänzungsband, Berlin.
15. Stresemann, E. (1927–1934): Handbuch der Zoologie. Aves. Vol. 7, Hälfte 2.
16. Weigold, H. (1926). Masse, Gewichte und Zug nach Alter und Geschlecht bei Helgoländer Zugvögeln. Wiss. Meeresunters. (Abteilung Vogelwarte), Neue Folge, 15. Abteilung Helgoland, No. 17, 1–73. Festschrift für Friederich Heincke.
17. Wilder, G. D. (1925). Migration Notes. The China Journal of Science and Arts, 3, 395–399.
18. —— (1934). Migration Notes. The China Journal, 21, 135–139.

# The Ottenby Bird Station

## Ottenby Bird Station Report No. 8

*Carl Edelstam*
*Stockholm*

[This is an abstract of a report that was planned for the Congress but had to be cancelled due to the enforced absence of the author. In my place a report was given at the Congress by Mr. Viking Olsson. Originally, I wrote my report to suit a set of colour slides, which cannot be included here, and so I have preferred to revise it considerably, centering on a few points that make up the "individuality" of Ottenby as compared with similar institutions abroad, and leaving additional space for the presentation of some data from our work in recent years to show what kind of material is accumulated here for the benefit of future research.]

After some years of tentative banding and observation, the south point of the island of Öland was chosen as the site of a bird station—the first one in Sweden—for which funds were granted to the SOF (Sveriges Ornitologiska Förening) by seven private donors in the spring of 1945. This is classical ground for ornithological research, having been visited by Linné on his voyage to Öland in 1741 and known later for the important studies by Gustaf Kolthoff on sex and age differences in migration habits among the waders. It is notoriously rich in birds, with a species-list totalling 335 for the nearest 20 square kms. (perhaps the highest number recorded in Scandinavia for such a small piece of land). And more especially, its passage-migrant fauna includes a large element moving in NW—SE direction which makes it a valuable and rather contrasting complement to the observation point at Falsterbo, in SW Sweden, where the SOF also carries out migration studies.

In the summer of 1946, the Station building was ready: a wooden bungalow 8 × 14 m., containing a living-room, a laboratory, three bedrooms with a total of eight beds, a kitchen, and ample cellar space. Its surroundings are seen in fig. 1, with the lighthouse immediately to the south, open

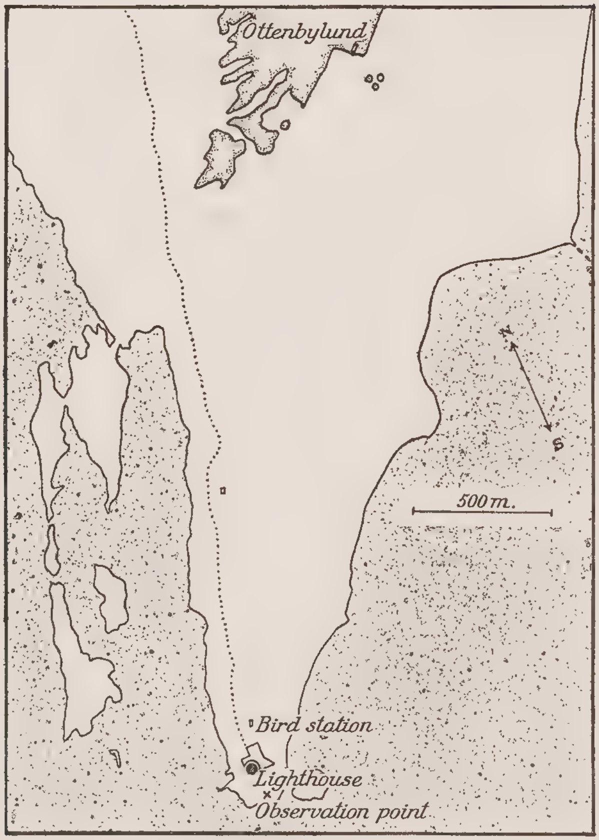


Fig. 1. Map showing the flat pasture-grounds of the south point of Öland, with the observation point, the lighthouse and its staff buildings, the Bird Station and, in the upper margin, the edge of the forest of Ottenbylund, where many birds take a rest before leaving the island. The path goes to the little village of Ottenby, situated by the main road 1 500 m. farther to the north.

ground to the east and west leaving a free view of the shores, and vast pasture-grounds north of it as far as the forest of Ottenbylund and the little village of Ottenby. The lighthouse tower, built in 1785, is the tallest in Scandinavia (125 ft.) and has a double 1 500 000 normal-light's electrical beam that turns around twice in a minute. It exerts a considerable attraction on birds passing by night in hazy weather, but deaths are not very numerous, thanks partly to the illumination of the tower by small lamps (as devised by Prof. Hugo Weigold, of the Vogelwarte Helgoland). The meteorological equipment of the lighthouse allows a continuous automatic registration of temperature, atmospheric pressure, and wind direction and intensity, invaluable for the analysis of the dependence of migration upon weather. Rainfall and cloudiness is also recorded regularly.

Since 1947, the activity of the Station has been generously supported by the State Research Council of Sweden. Although it might have been possible with this support and other money available to carry out ornithological work on a small scale throughout the year, we considered it more promising to concentrate upon one single phase of the migration. Following this plan, the Station has been manned during the last few years from about June 1st to October 31st, a period covering the southward movement almost from its beginning and to a time when there is already a large component of "Winterflüchtlinge" among the birds passing. The staff consists of three or four persons: one field observer, and 2–3 banders of whom the senior one should be able to relieve the observer when necessary. Because of the very trying kind of work, this staff is changed each month as a rule—a procedure that may appear disadvantageous at first sight but that has proved very satisfactory in educating a generation of competent migration students, who can return here or take up their own work at other places in the country. This last point is not without importance; indeed, it appears highly desirable to get regular information on a small scale—*e.g.*, by whole-day observation once a week—from some scattered places in addition to the large body of data accumulated at the chief points of migration study in Sweden: Ottenby and Falsterbo. Such activity would complete our picture of the general course of bird migration over our country, and it has already proved valuable for the registration of the irregular "irruptions" of certain species as well as for the study of local modifications in migration behaviour. The recent work of Tore Andersson and Dag Hannerz at Väddö (Uppland) (Rospiggens Grisslehamnsnummer, 1949, p. 27) and of Folke Hanström at Karlshamn in Blekinge (Blekingeboken, **24**: 124, 1946) is a promising example of this kind.

The problems tackled at Ottenby are the same as those facing migration students in many other places. Rather than reviewing them here—which would largely mean a repetition of points already stressed in this volume—I shall try to give an idea of the general character of the field work carried out at the Station and of the kind of material that is put at the disposal of the SOF through its recent activity.

Banding is carried out with the aid of a "Helgoland trap" on open ground in the station garden, other big passerine traps in the lighthouse gardens, a few "hawk traps," 15–20 wire cages on the wrack-beds of the shore, and some experimental traps of other kinds. Among these devices, the wire cages attract major interest due to their very specialized

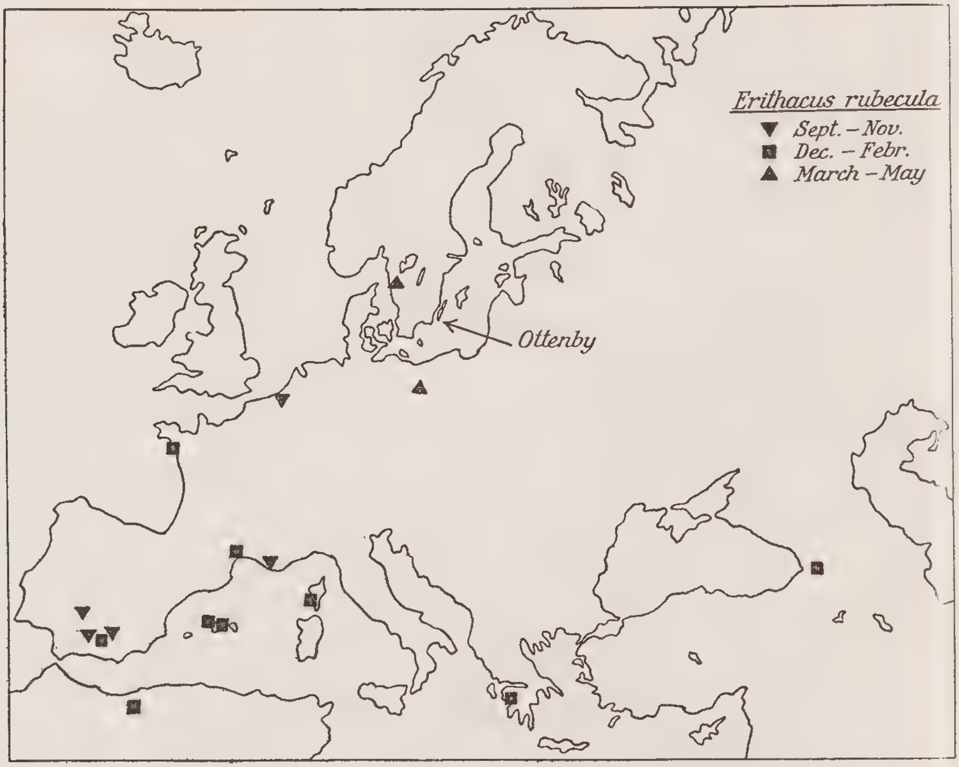


Fig. 2. Recoveries up to Dec. 1, 1950, of robins (*Erithacus rubecula*) trapped and banded on autumn passage at Ottenby 1937–49. The recoveries were made within 30 days—30 months from the date of marking, the mean being 10 months. It seems probable from this figure that some recoveries still remain to be made at least from the '49 markings, so that the rate of returns (now 16/3177 = 0.5 per cent) will finally amount to about 0.7 per cent.

operation and the large number of individuals of a few species that will be caught in them when conditions are favourable (the position of the level of the water is of special importance). For instance, we owe to these cages the banding in 1948 of 71 *Arenaria interpres*, 64 *Calidris minuta*, and 76 *C. temminckii*; in 1949 of 325 *Anthus pratensis*, 80 *A. cervinus*, 527 *A. spinoletta*, 1 348 *Motacilla alba*, 119 *Calidris canutus*, 3 552 *C. alpina*, and 169 *C. ferruginea*; and in 1950 of 164 *Philomachus pugnax*, 535 *Tringa glareola*, and 268 *T. totanus*. It may be seen that these are partly such species, which are otherwise only rarely banded and for which the speed of migration and the details of destination are thus largely unknown (*cf.* fig. 3). For *Calidris alpina*, it has indeed been possible to establish, through

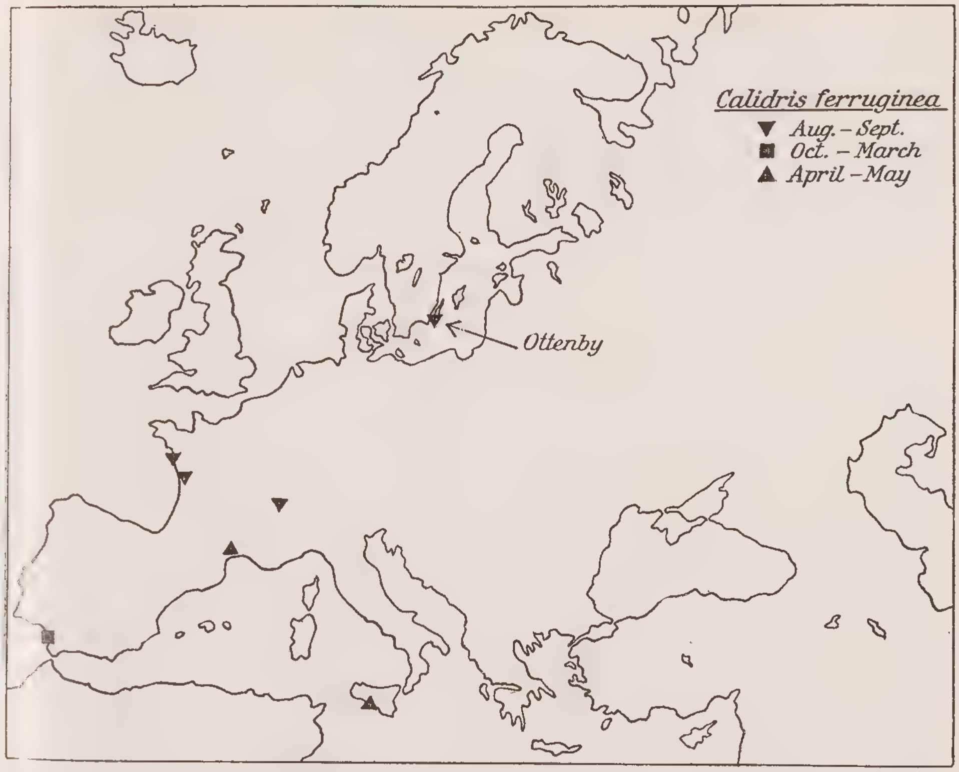


Fig. 3. Recoveries up to Dec. 1, 1950, of curlew-sandpipers (*Calidris ferruginea*) trapped and banded on autumn passage at Ottenby 1937–49. A considerable speed of passage from the Baltic to France is indicated by the recovery of 3 individuals in the latter country after 7, 12, and 14 days, respectively; but still the average time within which the returns were reported amounts to 12 months, due to the others coming considerably later (for instance, the control at Ottenby was made after 35 months). The final recovery rate is estimated at about 2 per cent for this species under present conditions, which would require one or two additional returns from the good catches in 1949, but clearly this figure cannot be relied upon very much with such a limited material as 424 markings.

recoveries at Ottenby, 19 separate cases of an individual keeping to the same migration route at least for two different years. This is interesting not only because of the general scarcity of such records for any species but also in view of the remote origin of these birds, presumably the N. Russian tundra. The catches also allow a quantitative estimate of the passage of each species that will often be more real than the figures obtained by direct observation of the migration. This is especially the case for the rarer *Calidris* species which are difficult to pick out from the ra-

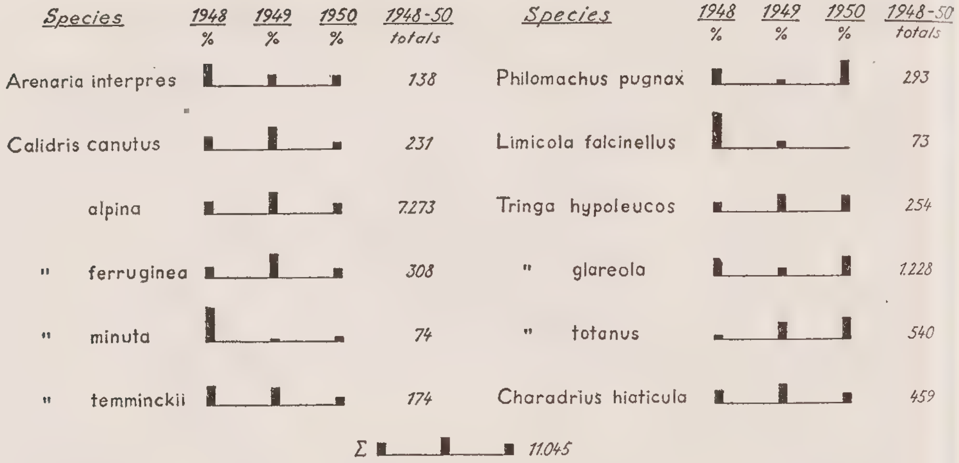


Fig. 4. Bar diagrams to show fluctuations in the autumn-passage of waders over Ottenby 1948–50 as indicated by the yearly differences in wire-cage catches. (From a material of more than 11 000 birds.) All species of which over 70 individuals were caught in the 3-year period have been included. The bars show the catch in each year reduced to per cent of the total catch of the species 1948–50 (absolute figures for the latter are given to the right). The diagram at bottom, showing the pooled percentage for all species and thus measuring the approximate efficiency of trapping in each year, may be used for reference; but the reader is reminded that these values are somewhat unduly influenced by one single species (*Calidris alpina*), so that if this species were excluded the pooled diagram would appear almost perfectly balanced.—It may be seen that while the values for some species (*e.g.*, *Tringa hypoleucos* and *Charadrius hiaticula*) are fairly stable, there are in other cases striking trends which, however, do not exhibit any interspecific conformity. Surely such fluctuations are sometimes spurious: an abnormal level of the water during the peak of passage may have influenced the catches of a certain species; or weather conditions may have caused the birds to remain at Ottenby longer than usual resp. to pass in numbers without resting. But when an influx of a certain species is noted over great parts of W. Europe, as often happens, other explanations are called for. An occasional large-scale change of migration route or a real change of population would reasonably be involved in these cases; but the lack of continuous observations in E. Europe and particularly in S. Russia leaves us uncertain about the state of things.

pidly passing flocks of *C. alpina* and *Charadrius hiaticula*, and for those species which leave chiefly by night. Finally, some of the birds caught in the autumn of 1950 were subjected to physiological and parasitological investigations by visiting scientists from abroad.

Much less attention has been paid to the banding of nestlings around the Station, in spite of the unusual richness of the local breeding fauna. About 90 per cent of the figures for banded nestlings is assignable to the nearby colonies of *Delichon urbica*, *Larus ridibundus*, and *Larus canus*, and to certain species of duck to which Notini's method of wing-marking (*cf.* Vår Fågelvärld **6**: 28, 1947) has been successfully applied. Only this intentional disregard of the resident birds has made it possible to carry out a program for intensive migration research with such limited means as have been hitherto available. It is important in this connection that we have also been free from the task of organizing banding activity in other parts of the country, with the time-consuming office work that follows such a task. On the contrary, rings were put at our disposal and the correspondence regarding the recoveries was handled by the Vertebrate Department of Riksmuseum (Stockholm).[1] This has been a great help to the Station Committee[2] in reducing office work to a minimum.

Since the establishment of the Station, great emphasis has been placed upon the field observations. It was soon realized that only regular whole-day observations could provide a reasonably adequate material for a study of the diurnal migration in its different aspects: the number of individuals and species of birds passing by, with its fluctuation from day to day and from year to year; the diurnal rhythm of each species and its dependence on light and weather conditions; flight direction and flight technique; social behaviour, etc. Thus, from 1947, the observation point 300 m. to the south of the Station (*cf.* fig. 1) has been manned, with few exceptions, from about half an hour before sunrise to half an hour after sunset during the whole working season. This program, laborious though it is, has well repaid the work spent on it. It is evident from the data assembled that observations restricted to the migration maximum in the morning hours and the secondary maximum in the evening, although fairly representative as far as the relative number of migrants between different days is concerned, will give quite a misleading picture of the migration of those species which have a less pronounced diurnal rhythm, or of those which will respond to certain weather situations by passing by in great numbers without regard to the hour. There are even some species showing a maximum about noon (*Apus apus*) or in the afternoon before the general evening migration (*e.g.*, some waders).

In order that the material of observations should be easily accessible for research work, the body of data for each year has been reduced to tables giving comprehensive information on the main course of migration at Ottenby from June to October. For the purpose of this paper, I have condensed some of these tables still further and shall conclude by presenting them here together with some brief explanations. They generally concern the "autumn" seasons of 1948–50, with an observation period of resp. June 2–Oct. 30, June 1–Oct. 31, and May 29–Oct. 31. As far as a column for 1947 has also been included, it should be noted that this year is not strictly comparable with the other ones on account of a difference in observation period (June 15–Nov. 14). However, this is not likely to influence appreciably the trends which these tables are intended to illustrate.

---

[1] Through the courtesy of its director, Prof. Hialmar Rendahl, and Miss Greta Westergren.

[2] The Ottenby Bird Station Committee was appointed by the SOF Committee in 1945 and consists of four persons, responsible for the activity of the Station: Gustaf Danielsson (practical management), Dr. Gunnar Svärdson (scientific planning), Bertil Haglund, and the author.

Tab. 1.

| Banded | 1937–47 | 1948 | 1949 | 1950 | M<br>1948 50 |
|---|---|---|---|---|---|
| Banded after trapping.... | 7 285 | 7 472 | 13 009 | 10 577 | 10 353 |
| Banded when young ..... | 524 | 1 799 | 1 050 | 985 | 1 278 |
| S | 7 809 | 9 271 | 14 059 | 11 562 | 11 631 |

Table to show the banding activity at Ottenby. The material from each year has been divided into two groups, one including those birds which have been banded after trapping and which will with few exceptions be passage-migrants, the other including those banded when young. The result of the tentative marking in 1937, 1938, 1946, and 1947 has been added together in one column; from 1948, when the trapping devices were put up to their present state, the results are given separately, and the mean values for these years have been calculated to the right. From records published, it seems that the yearly totals, as well as the separate figures for banded passage-migrants, are the highest ones attained so far by any bird-trapping station. As to the recovery percentages, a pooled value would be of little interest, but some specific figures may be mentioned. Thus, among species of which three or more recoveries have been reported, the highest percentage is attained by *Capella gallinago* (3 returns up to Dec. 1, 1950, from 13 markings in 1937–50 = 23 %—certainly an unreliable figure, but perhaps not far from reality because of the intensive hunting of this bird) and by *Accipiter nisus* (5 returns up to Dec. 1, 1950, from 44 markings in 1937–49 = 11 %). Second among the waders, apart from some definitely unreliable figures for *Numenius*, *Limosa*, and *Recurvirostra*, ranks *Tringa totanus* with 3 % (18 returns up to Dec. 1, 1950, from 607 markings in 1937–50). Considering the bottom values, the most disappointing case is perhaps the lack of recoveries from the 628 markings of *Lanius collurio* in 1937–50; and the happiest manifestation of chance is the recovery in Spain of one out of 7 *Muscicapa parva* banded in 1937–49.

Tab. 2.

| Order/Suborder | 1937–47 | 1948 | 1949 | 1950 | M 1948–50 |
|---|---|---|---|---|---|
| Passeriformes | 59 | 57 | 68 | 62 | 62 |
| Apodiformes | 1 | 1 | 1 | 1 | 1 |
| Piciformes | 1 | 3 | 3 | 2 | 3 |
| Falconiformes | 4 | 2 | 4 | 3 | 3 |
| Anseriformes | 9 | 8 | 4 | 7 | 6 |
| Charadrii | 19 | 19 | 21 | 23 | 21 |
| Lares | 6 | 5 | 3 | 6 | 5 |
| Galliformes | 1 | 1 | 1 | 1 | 1 |
| Other groups | 4 | 5 | 5 | 6 | 5 |
| S | 104 | 101 | 110 | 111 | 107 |

In this table is shown the number of species banded at Ottenby in different years and their systematic distribution. Groups usually represented by less than three species have only been tabled separately if the annual catch exceeds 10 individuals on the average.—Comparing with tab. 5 a, we can see that nearly as many species of waders are banded each year as are seen on diurnal migration. In fact, among the waders listed as diurnal migrants during one or more of the autumn seasons 1947–50 only six species have failed to go into the wire-cages at least once, and of these, two could be added to the ringing-list by marking young birds of the local population (*Numenius arquata*, *Recurvirostra*), while the other four have not yet been banded (*Limosa limosa*, *Tringa nebularia*, *Pluvialis apricaria*, *P. squatarola*). On the other hand, two species which have never been recorded on daylight passage because of a preference for nocturnal migration or because of their scarcity, have been occasionally trapped and banded (*Lymnocryptes*, *Xenus*). Turning to the passerine birds, an equally close relationship is found between banding and daylight passage. Only four species recorded on diurnal migration have not yet been trapped at the Station: *Corvus frugilegus*, *Plectrophenax*, *Lullula*, and *Riparia*. In their place, a number of exclusively nocturnal migrants are regularly banded, so that there are still more species of Passeriformes listed in this table than in tab. 5 a. For other groups, such as the Falconiformes and Anseriformes, there is a marked discrepancy in the other direction between the present table and tab. 5 a. The figures for the ducks and gulls would be still lower, were it not for the regular banding of the young of several resident species.

Tab. 3.

| Order/Suborder | 1937–47 | 1948 | 1949 | 1950 | M 1948–50 |
|---|---|---|---|---|---|
| Passeriformes | 4 973 | 5 256 | 8 924 | 8 017 | 7 399 |
| Apodiformes | 423 | 102 | 45 | 52 | 66 |
| Piciformes | 3 | 7 | 61 | 9 | 26 |
| Falconiformes | 20 | 7 | 30 | 57 | 31 |
| Anseriformes | 180 | 159 | 99 | 138 | 132 |
| Charadrii | 1 893 | 3 457 | 4 793 | 3 016 | 3 755 |
| Lares | 254 | 263 | 87 | 225 | 192 |
| Galliformes | 56 | 9 | 8 | 17 | 11 |
| Other groups | 7 | 10 | 12 | 31 | 17 |
| S | 7 809 | 9 270 | 14 059 | 11 562 | 11 630 |

Table giving the quantities of birds banded at Ottenby since 1937 and their systematic distribution. Space has not allowed a separation in this table of individuals banded after trapping and those banded as young birds, but the latter group is negligible except for the Passeriformes, Anseriformes, and Lares. The abrupt rise of the woodpecker curve in 1949 was due to an irruption of *Dendrocopos major*.—A partial specification of the figures given here for the Charadrii may be found in fig. 4. As regards the 1950 figure for Passeriformes, the reader is referred to the comments in Table 4 on the banding of spring migrants during this year.

Tab. 4.

| Species | 1937–47 | 1948 | 1949 | 1950 | M 1948–50 |
|---|---|---|---|---|---|
| *Sturnus vulgaris* | 36 | 189 | 441 | 956 | 529 |
| *Carduelis spinus* | 4 | 6 | 519 | 19 | 181 |
| *Anthus spinoletta* | 95 | 84 | 527 | 159 | 257 |
| *Motacilla alba* | 747 | 328 | 1 348 | 1 260 | 979 |
| *Phylloscopus trochilus* | 175 | 76 | 584 | 1 059 | 573 |
| *Phoenicurus phoenicurus* | 362 | 266 | 446 | 541 | 418 |
| *Erithacus rubecula* | 1 175 | 1 137 | 865 | 772 | 925 |
| *Delichon urbica* | 19 | 1 276 | 789 | 583 | 883 |
| *Calidris alpina* | 1 080 | 2 141 | 3 552 | 1 580 | 2 424 |
| *Tringa glareola* | 230 | 476 | 217 | 535 | 409 |
| S | 3 923 | 5 979 | 9 288 | 7 464 | 7 577 |

In this table are listed those 10 species of which a total of more than 500 individuals were banded during one or more of the years 1948-50. Many of these species are regularly found among those topping the ringing records; others, like *Carduelis spinus*, are represented here only because they have been trapped on an exceptional scale during a single irruption year. The high figures for *Delichon* are almost exclusively due to the banding of residents (mostly nestlings), whereas for the other species this has been of no importance. The 1950 values for *Phylloscopus trochilus* and *Phoenicurus phoenicurus* are largely due to the extension of ringing activity during this year to the spring migration period in May; to the quantity of other species tabled, spring banding added little or nothing.—A daily figure of more than 500 for a single species has only been attained once: on Aug. 1st, 1949, 654 birds were banded among which were 604 *Calidris alpina.*

Tab. 5 a.

| Order/Suborder | 1947 | 1948 | 1949 | 1950 | M |
|---|---|---|---|---|---|
| Passeriformes | 32 | 38 | 38 | 36 | 36 |
| Apodiformes | 1 | 1 | 1 | 1 | 1 |
| Falconiformes | 17 | 13 | 16 | 15 | 15 |
| Anseriformes | 22 | 20 | 20 | 22 | 21 |
| Colymbiformes | 2 | 2 | 2 | 2 | 2 |
| Columbiformes | 4 | 3 | 3 | 3 | 3 |
| Charadrii | 25 | 26 | 27 | 27 | 26 |
| Grues | 1 | 1 | 1 | 1 | 1 |
| Lares | 14 | 13 | 14 | 13 | 14 |
| Other groups | 3 | 4 | 7 | 6 | 5 |
| S | 121 | 121 | 129 | 126 | 124 |

Table showing the species-distribution of passage-migrants at Ottenby in autumn, as indicated by daylight observations of birds disappearing over the sea in E—S—W direction. The arithmetical means are given in the outer right column, the totals at bottom. Groups represented by but one or a few species have been separately tabled only if they are usually present in a fairly great number of individuals (*cf.* tab. 6 a).—Clearly, the total number of species observed each year at Ottenby is much higher than that given here, due particularly to the presence of numerous species of exclusively nocturnal migrants resting in the neighbourhood.

Tab. 5 b.

| Order/Suborder | 1947 | 1948 | 1949 | 1950 | M |
|---|---|---|---|---|---|
| Passeriformes (mostly *Hirundo, Delichon, Riparia*) | 3 | 4 | 2 | 6 | 4 |
| Apodiformes (*Apus*) | 1 | 1 | 1 | 1 | 1 |
| Falconiformes (mostly *Falco, Accipiter*) | 3 | — | 3 | 5 | 3 |
| Other groups | — | 1 | 1 | 12 | 4 |
| S | 7 | 6 | 7 | 24 | 11 |

Table showing the species-distribution of passage-migrants recorded on reversed migration at Ottenby in autumn, as indicated by daylight observations of birds appearing over the sea from E—S—W and moving in over land in W—N—E (usually rather straight N) direction. This phenomenon is usually connected with winds from the north, which is a rather rare event on Öland; and it is illuminating from an aerodynamical point of view that the birds involved are mostly swallows, martins, swifts, and birds of prey, which are all characterized by a gliding or soaring flight. The immediate origin of these north-going migrants is rarely quite clear. Often it seems that they have really tried to leave Öland in a normal direction although at altitudes out of field-glass range from the observation point, and later lost height and been forced to return along the sea level. However, the Swift—and to some extent also the Swallow and the Martins—seem generally inclined to move against the wind and will thus continue to fly northwards even over great land areas if the northerly wind remains steady for some time. Under such circumstances, the birds observed on reversed migration at Ottenby might be of a more distant origin.—All of the species indicated here were also observed on normal southward migration.

**Tab. 6 a.**

| Order/Suborder | 1947 | 1948 | 1949 | 1950 | M |
|---|---|---|---|---|---|
| Passeriformes | 110 900 | 176 300 | 196 300 | 260 400 | 186 000 |
| Apodiformes | 137 500 | 97 900 | 57 700 | 119 000 | 103 000 |
| Falconiformes | 870 | 570 | 1 250 | 1 360 | 1 010 |
| Anseriformes | 48 100 | 40 300 | 68 700 | 51 300 | 52 100 |
| Colymbiformes | 260 | 40 | 790 | 670 | 440 |
| Columbiformes | 3 450 | 3 560 | 5 440 | 7 880 | 5 080 |
| Charadrii | 30 400 | 28 200 | 52 100 | 47 700 | 39 600 |
| Grues | 1 900 | 1 260 | 3 420 | 2 210 | 2 200 |
| Lares | 10 600 | 11 000 | 29 100 | 15 600 | 16 600 |
| Other groups | 20 | 10 | 70 | 30 | 30 |
| S | 344 000 | 359 100 | 414 900 | 506 200 | 406 100 |

Table to show the numbers of south-bound passage-migrants at Ottenby in autumn, as indicated by daylight observations (*cf.* text of tab. 5 a). All figures (also means and totals) have been rounded off: below 10 000, to the nearest 10; above 10 000, to the nearest 100. —It is easily seen that the total quantity is not comparable with that reported from Rossitten or Falsterbo; but as the specific composition is largely different, individual figures will still be higher than at these places (as compared with Falsterbo, esp. *Motacilla alba* and *Apus apus*).

**Tab. 6 b.**

| Order/Suborder | 1947 | 1948 | 1949 | 1950 | M |
|---|---|---|---|---|---|
| Passeriformes (mostly *Hirundo, Delichon, Riparia*) | 8 820 | 750 | 230 | 930 | 2 680 |
| Apodiformes (*Apus*) | 1 500 | 2 390 | 4 500 | 5 810 | 3 550 |
| Falconiformes (mostly *Falco, Accipiter*) | 40 | — | 20 | 20 | 20 |
| Other groups | — | — | 120 | 280 | 100 |
| S | 10 360 | 3 140 | 4 870 | 7 040 | 6 350 |

Table 6 b shows the numbers of north-bound passage-migrants at Ottenby in autumn, as indicated by daylight observations (*cf.* text of tab. 5 b).—Only for one species and in one year did the number of individuals moving to the north exceed the number of those seen moving in the normal direction (*Delichon urbica*, 1947: + 2 840, — 8 160). On their final migration in that autumn the House Martins would have avoided a passage over Ottenby, or moved south at heights where they could not be seen by the observer.

Tab. 7.

| Species | 1947 | 1948 | 1949 | 1950 | M |
|---|---|---|---|---|---|
| *Sturnus vulgaris* | 56 300 | 33 700 | 59 200 | 105 400 | 63 700 |
| *Chloris chloris* | 70 | 3 000 | 11 600 | 1 430 | 4 030 |
| *Carduelis cannabina* | 7 470 | 22 500 | 30 200 | 20 500 | 20 200 |
| *Fringilla coelebs* | 4 100 | 18 600 | 3 530 | 20 500 | 11 700 |
| *F. montifringilla* | 5 450 | 12 700 | 8 920 | 1 890 | 7 240 |
| *Alauda arvensis* | 2 100 | 1 970 | 10 100 | 3 790 | 4 490 |
| *Motacilla alba* | 17 000 | 22 200 | 34 500 | 36 400 | 27 500 |
| *Hirundo rustica* | 3 580 | 3 850 | 3 850 | 11 700 | 5 750 |
| *Delichon urbica* | 2 840 | 9 400 | 7 120 | 18 400 | 9 440 |
| *Riparia riparia* | 2 270 | 3 930 | 1 000 | 15 800 | 5 750 |
| *Apus apus* | 137 500 | 97 900 | 57 700 | 119 000 | 103 000 |
| *Anas penelope* | 5 000 | 9 950 | 12 400 | 17 600 | 11 240 |
| *Calidris alpina* | 8 000 | 8 630 | 23 300 | 20 200 | 15 000 |
| *Larus ridibundus* | 6 350 | 5 010 | 13 100 | 8 500 | 8 240 |

This table includes 14 species which during one or more of the observation years 1947–50 reached a yearly total of more than 10 000 individuals counted on diurnal migration to the south. (Figures rounded as in tab. 6.) The list is not quite complete: some species of diving duck, which have—or may have—reached similar figures, had to be disregarded because a large proportion of the individuals of this group could not be specifically determined on account of their great distance from the observer; and this in turn means that the totals noted for each of these species are, to a varying degree, too low and are not suitable for comparison with those of other species. (In principle, this reasoning also applies to the swallows and to *Anas penelope*; but the error introduced here is of little significance.)—When comparing the yearly totals for all birds, given at the bottom of tab. 6 a, it is seen that, on the average, more than half the number of autumn-migrants counted at Ottenby represent four single species: *Apus apus*, *Sturnus vulgaris*, *Motacilla alba*, and *Carduelis cannabina*. But it is also evident that the 14 species of this table are not all among the 14 most common migrants at Ottenby. Some of them (*Chloris*, *Alauda Hirundo*, *Riparia*) are represented here only because their number has risen abruptly in a single year from a normal level of 3 000–4 000 or less. The possible causes of such incidents are discussed in the text of fig. 4.

Tab. 8.

| Species | 1947 | 1948 | 1949 | 1950 | M |
|---|---|---|---|---|---|
| *Sturnus vulgaris* | — | — | — | 2 | < 1 |
| *Fringilla coelebs* | — | — | — | 1 | < 1 |
| *Riparia riparia* | — | 3 | — | 1 | < 1 |
| *Apus apus* | 4 | 3 | — | 5 | 3 |
| S | 4 | 3 | — | 9 | 4 |

Table to show how many times an individual species has been recorded as passing over Ottenby in more than 10 000 specimens in one day of its autumn migration. It is seen from a comparison with tab. 7 that those two species, which top the list of yearly totals, are also ahead of the others with regard to the number of days in which a large-scale passage takes place (*Apus*, *Sturnus*). On the other hand, *Fringilla coelebs* only ranks sixth on the list of yearly totals, and *Riparia* comes still lower. Their presence in this table is due to the well-known, but not well-explained fact that many species, although extending their migration over a considerable period, tend to concentrate numerically to one or a few days in the season. This behaviour —fittingly called "lavinfenomenet," or the avalanche phenomenon, by Svärdson (1950 b)— is shown to a varying degree by representatives of most bird groups. However, in some groups (*e.g.*, gulls and terns) it is quite rare and may even be reversed; that is, the more or less moderate hump that usually occurs at the centre of any migration curve, where the dates are plotted on the abscissa, is subnormally low or even absent. Such birds will appear in the observer's record on a relatively larger number of days than the typical "avalanche species", although the actual length of the migration period, as counted from the first to the last day of observation, will not necessarily differ between the two groups.

Tab. 9.

| | | | | | |
|---|---|---|---|---|---|
| *Sturnus vulgaris* | 92 | *Anas platyrhynchos* | 53 | *Charadrius hiaticula* | 63 |
| *Hirundo rustica* | 62 | *A. penelope* | 57 | *Haematopus ostralegus* | 61 |
| *Apus apus* | 84 | *A. acuta* | 70 | *Larus ridibundus* | 85 |
| *Accipiter nisus* | 60 | *Numenius arquata* | 84 | *L. canus* | 75 |
| *Tadorna tadorna* | 63 | *Calidris alpina* | 80 | *L. fuscus* | 63 |

In this table are listed those species which were seen performing migration movements during more than one third of the number of observation days in 1950 (May 29–Oct. 31: 156 days). Only 5 out of these 15 species were recorded on passage more than half the number of days. Comparing with tab. 7, it is seen that the two quantitatively dominating birds of this year (*Apus*, *Sturnus*) are among those topping the list; this is primarily due to certain characteristics of their migration, involving irregular weather-movements and a regular "Zwischenzug," respectively. We also observe that 5 out of the 10 most common species are not present here. In their place, we find some species which did not reach a yearly total of more than 1 000–4 000, in one case (*Accipiter nisus*) 660 migrants. This should be seen in the light of what is said in the text of tab. 8 on the irregularity of the relationship between high daily figures, high seasonal figures, and the length of the migration period.

## References

Only the papers mentioned below are exclusively—or almost exclusively—related to the bird migration at Ottenby (short notes and some older reports of limited interest excluded). For details about banding and observations, and for photographs of the trapping devices, the reader is especially referred to the annual reports of the Station.

Bergman, G., 1948. Sträck, återflygning och övernattning hos sädesärlan (*Motacilla alba*) under hösten vid Ölands södra udde. (Zug, Rückflug und Schlafplätze von *Motacilla alba* im Herbst an der Südspitze Ölands.) OBS report no. 3. — Vår Fågelvärld **7**: 57.

Bergström, U. & G. Svärdson, 1938. Ringmärkningar och fågeliakttagelser vid Ölands södra udde under höststräcket 1937. — Fauna o. Flora **33**: 1.

1939. Ringmärkningar och fågeliakttagelser vid Ölands södra udde under höststräcket 1938. — Fauna o. Flora **34**: 97.

Danielsson, G., C. Edelstam & G. Svärdson, 1947. Ottenby fågelstation, dess tillkomst och verksamhet år 1946. (OBS 1st annual report: 1946.) OBS report no. 1. — Vår Fågelvärld **6**: 38.

Hasselblad, V., 1935. Flyttfågelstråk. — Stockholm.

Hylbom, R., 1951. Daily Ringing Figures and Passing Frequency in small Passerines. OBS report no. 9. — Proc. 10th Int. Congr. Orn.: 310.

Kolthoff, G., 1897. Zur Herbstwanderungen der nordischen Sumpfvögel über die Insel Öland. — Festskrift till Wilhelm Lilljeborg. Uppsala.

Svärdson, G., 1943. Flyttfågelforskning och behovet av svenska fågelstationer. — Sveriges Natur, Årsbok **34**: 89.

1948 a. Verksamheten vid Ottenby fågelstation 1947. (OBS 2nd annual report: 1947.) OBS report no. 2. — Vår Fågelvärld **7**: 25.

1948 b. Redogörelse för anslag till Sveriges ornitologiska förening. — Statens naturvetenskapliga forskningsråds årsbok **1**: 51.

— — 1949 a. Skruvflykt hos flyttande måsar. (Gyrations performed by migrating gulls.) OBS report no. 4. — Vår Fågelvärld **8**: 13.

— 1949 b. Verksamheten vid Ottenby fågelstation 1948. (OBS 3rd annual report: 1948.) OBS report no. 5. — Vår Fågelvärld **8**: 97.

— 1950 a. Verksamheten vid Ottenby fågelstation 1949. (OBS 4th annual report: 1949.) OBS report no. 6. — Vår Fågelvärld **9**: 11.

— 1950 b. Redogörelse för anslag till Sveriges ornitologiska förening. — Statens naturvetenskapliga forskningsråds årsbok **3**: 82.

— — 1951 a. Ny giv i sträckfågelforskningen. — Svensk Jakt **89**: 111.

— — 1951 b. Verksamheten vid Ottenby fågelstation 1950. (OBS 5th annual report: 1950.) OBS report no. 7. — Vår Fågelvärld **10**: 97.

— — 1951 c. Swift movements in summer. (OBS report no. 10.) — Proc. 10th Int. Congr. Orn.: 335.

# Migration Period of Some Passerines Revealed by Daily Ringing Figures at Ottenby

Ottenby Bird Station Report No. 9

*Richard Hylbom*

*Zoological Institute, Stockholm*

The passage of diurnal migrants may be observed in the field and the birds counted more or less exactly, depending on their frequency and the topography of the site used. In recent years much information regarding passing frequency in Sweden has been obtained by the Swedish Ornithological Society at both its Bird Stations, Ottenby and Falsterbo.

Many small passerine birds, however, migrate at night and their daily number cannot be counted directly. Some indirect method must, therefore, be used to reveal their normal passage from its beginning to its end at a certain locality. As a fraction of the nocturnal migrants passing a certain area normally alight to rest until the next night, there is a possibility of getting information regarding the passage by counting the number of individuals resting daily within a defined area. This is hard work, as a lot of the small birds are difficult to identify when seen at a distance and their total number may be absolutely impossible to state when they are frightened and flying around from bush to bush in a large garden.

The comparatively small garden at Ottenby Bird Station is more or less filled each night during the autumn by small passerine birds resting. The number of birds which alight in the garden depends on two factors the first being the number of birds actually in the air and the second theweather during the night. If visibility is bad quite a number of birds may stop their journey and a high proportion of the passing birds alight to rest when they meet the open sea, but when the weather is fine most of them will continue, providing only a few resting specimens next morning (Bergström and Svärdson 1939).

The birds resting in the lighthouse garden at Ottenby Bird Station are mostly trapped and ringed during the following day. In this way the number of resting birds may be roughly expressed by the daily ringing figures in the files of the Station. The equipment for trapping has been more or less

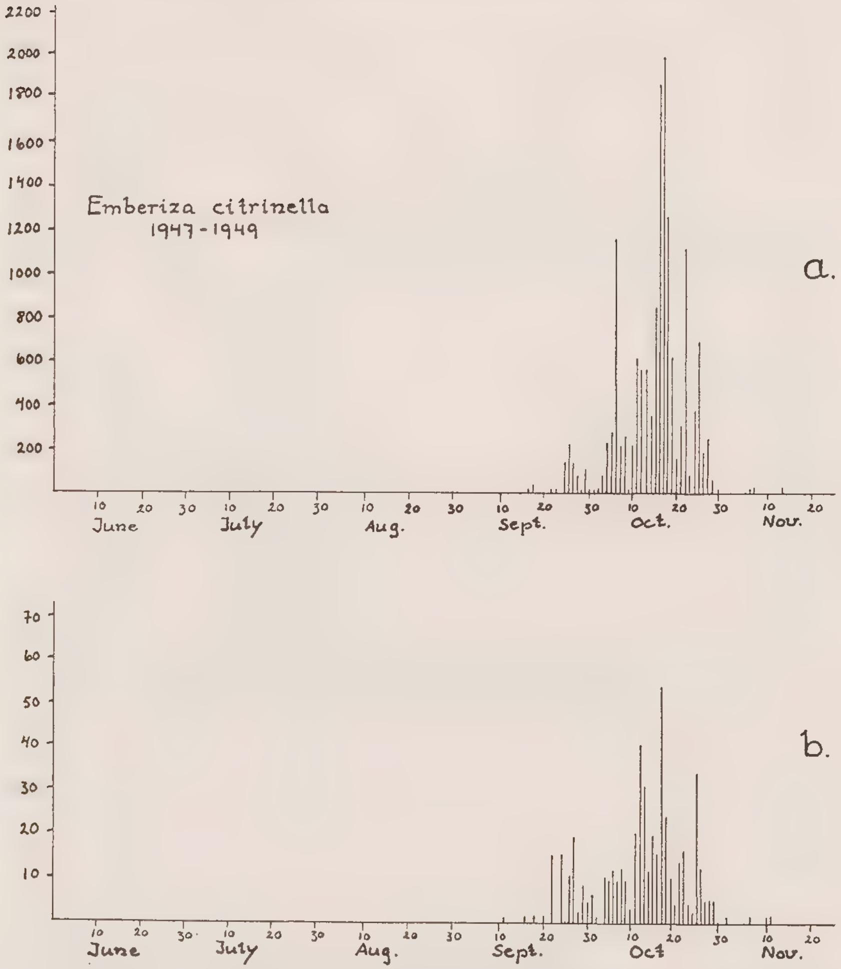


Fig. 1 and 2. Passing frequency of *Emberiza citrinella* and *Motacilla alba* in the seasons 1947–1949 as illustrated by the sum of birds observed departing (a) and the sum of specimens ringed daily (b).

the same during the last three seasons, when the great majority of birds, as yet ringed, have been trapped.

The method tested here for showing the normal passage of nocturnal migrants, has, therefore, been to select the number of birds ringed each day and add these figures to those obtained from other years. If all the birds ringed yearly, say on the 1st of August, are added to produce a single sum, chance fluctuations arising from weather must be increasingly eleminated. If all the days are dealt with in this manner the result ought to be

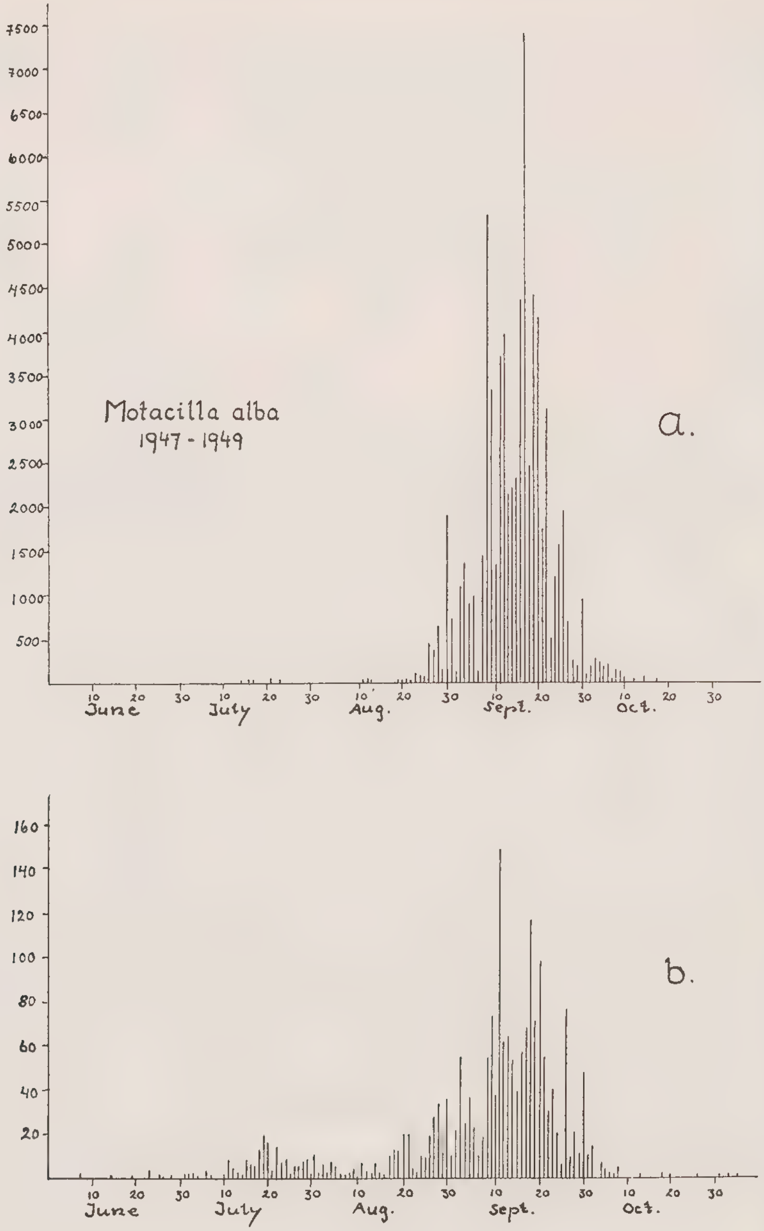

Motacilla alba
1947 - 1949
a.
7500
7000
6500
6000
5500
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
10 20 30 10 20 30 10 20 30 10 20 30 10 20 30
June
July
Aug.
Sept.
Oct.
b.
160
140
120
100
80
60
40
20
10 20 30 10 20 30 10 20 30 10 20 30 10 20 30
June
July
Aug.
Sept.
Oct.

Fig. 2.

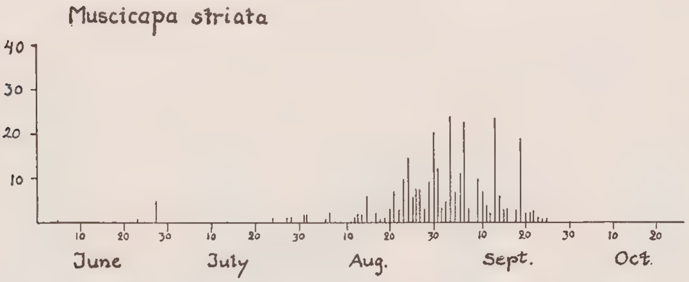


Fig. 3.

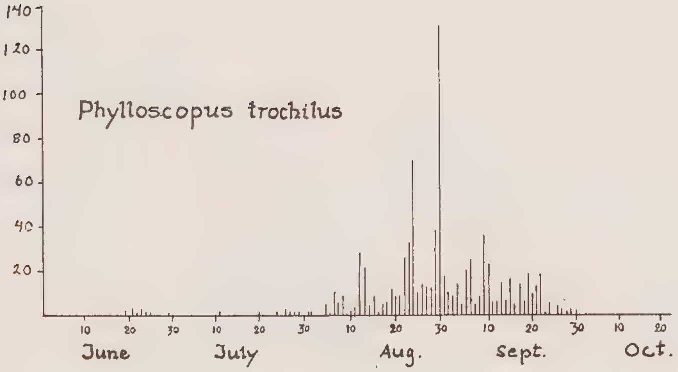


Fig. 4.

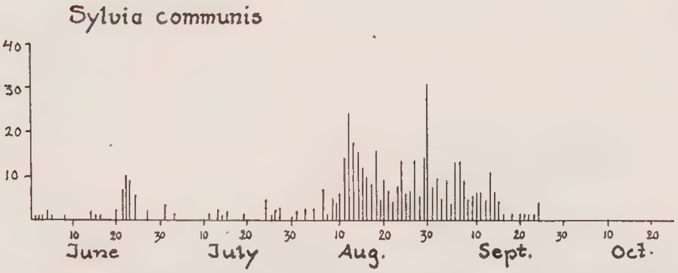


Fig. 5.

Fig. 3–11. Totals of the number of birds ringed per day at Ottenby for respectively *Muscicapa striata, Phylloscopus trochilus, Sylvia communis, Lanius collurio, Sylvia curruca, Muscicapa hypoleuca, Sylvia borin, Phoenicurus phoenicurus* and *Erithacus rubecula.*

a "normal curve" for the species' passage. The more birds that are trapped and the more different years involved, the more levelled the curve must be. Of course, variations between the different years according to the main waves of birds are concealed in this "summation curve," which tends to be broader at the base than any single year's curve. But in the case of nocturnal migrants, it seems to be impossible to reveal any single year's

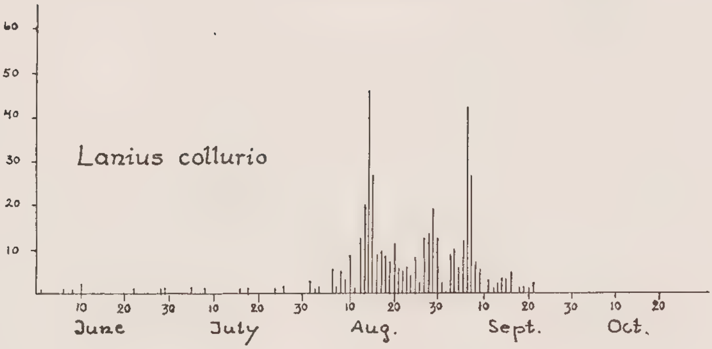


Fig. 6.

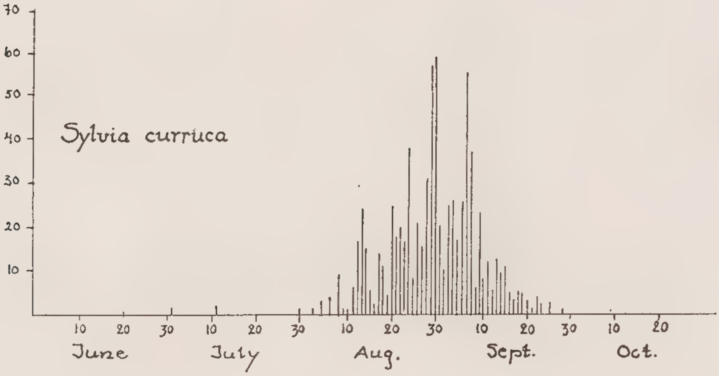


Fig. 7.

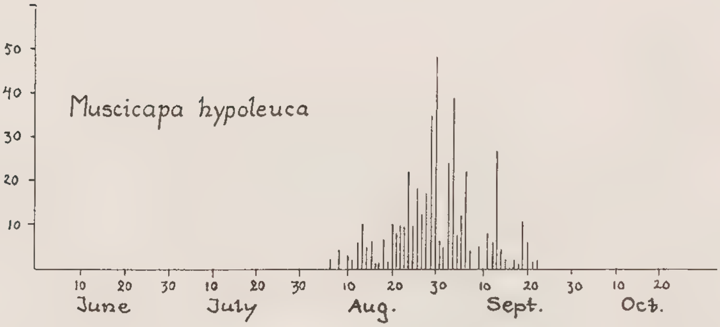


Fig. 8.

passage owing to the fact that weather fluctuations must then be very dominant.

It might also be added that the 'human factor' in this case is very small indeed, since the traps are manipulated every day during the season until it is judged that very few unmarked birds remain in the garden.

In order to test the method, a comparison has been made of the ringing

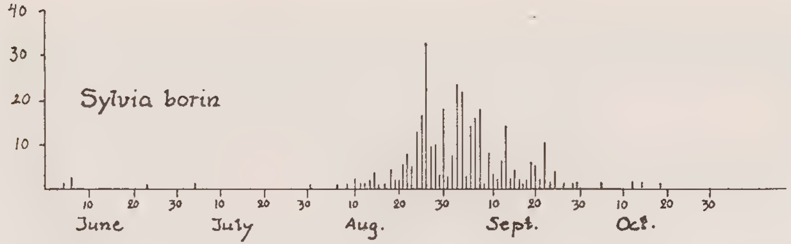


Fig. 9.

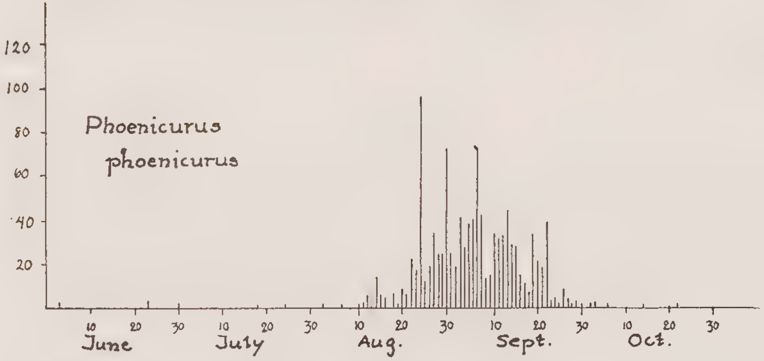


Fig. 10.

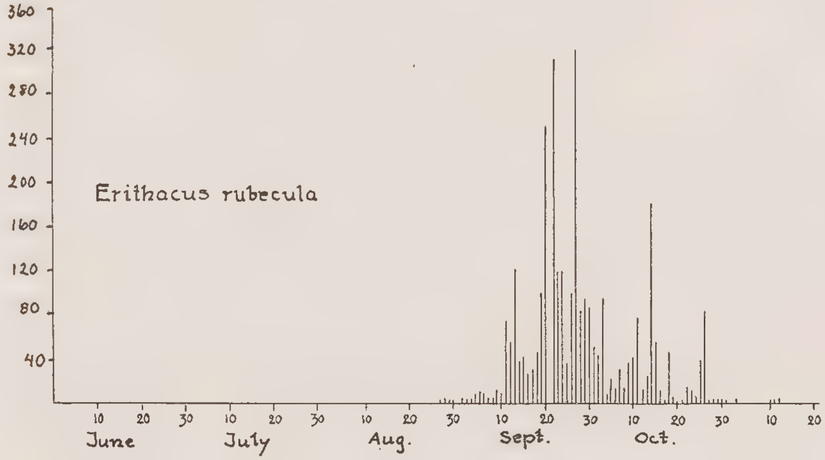


Fig. 11.

data and the observation data on some birds which are diurnal migrants and trapped in large numbers. For these birds, all passing birds observed have been added daily in a corresponding manner and so a correlation between the passage observed and the ringing performed is obtained. *Emberiza citrinella* and *Motacilla alba* have been selected, since the number ringed is highest for these species of diurnal passerine migrants. The result is shown in fig. 1 and fig. 2. The coincidence seems to be rather good, except for the fact that young, wagtails roam about before actual migration and during this period often go into our traps. Otherwise the "ringing method" is as good as the "observation method," when normal passage frequency is considered.

In fig. 3–11 some more diagrams are given of true nocturnal migrants for which no actual observations can be made. A few ringed birds which were known to be breeding in the locality, fledglings etc. have, of course, been eliminated from the totals, which include only birds presumably on migration at Ottenby.

The diagrams show during which period of the year the respective species pass Ottenby. It is noticeable that the passage is generally extended over a considerable time. It might be best to spare more conclusions as to the details for some years, as these diagrams, of course, must gain in probability for each consecutive year. The purpose of this paper has only been to present the method and provide stimulus for the preparation of similar curves for other stations. Obviously, if there were some more stations presenting corresponding curves from the Continent of Europe, some interesting information about general migration speed would be obtained.

## Reference

Bergström, U. and Svärdson, G. 1939. Ringmärkningar och fågeliakttagelser vid Ölands södra udde under höststräcket 1938. Fauna och Flora 34: 97–110, 135–156.

# The migration of birds of prey in southern Sweden, particularly at Falsterbo

*Gustaf Rudebeck*

*Zoological Institute, Lund, Sweden*

In the migration seasons birds of prey pass over southern Sweden, especially over Scania (Skåne), the southernmost province of the country, in very large numbers. So far, only the autumn migration has been thoroughly studied. The migrating birds generally move in a south-southwesterly direction over the interior of the country, but, since the birds dislike flying over large areas of open water, the coasts form very effective guiding lines. Along the western coast of Scania the birds move approximately in a southerly direction, and along the southern coast they fly due west. This causes a very marked concentration of migratory birds on the Falsterbo peninsula in the southwestern corner of Sweden. At this point they leave the country and cross the sea, usually in a west-southwesterly direction towards the Danish Isles.

The birds migrating over Falsterbo come from breeding places in Sweden and probably also, to a certain extent at least, from Finland and northwestern Russia. However, for most species the "recruiting area" is not yet satisfactorily known, and reliable data on the number of breeding pairs of each species in the area in question are available only in a few cases. Nevertheless, the general knowledge of the size of the breeding populations compared with the number of migrants passing Falsterbo, permits certain conclusions as to the degree of concentration, the influence of guiding lines, etc. And of course the field observations have yielded a wealth of data concerning the migratory habits of each species, the relation between migration and weather, the interrelationship between different species, and other items. Some of these questions are discussed in Rudebeck 1950, and a more detailed treatment on the subject is in progress.

It is evident, that the degree of concentration is very different in different species. The osprey, *Pandion haliaetus,* and the harriers *Circus aeruginosus* and *Circus cyaneus,* are not very frequent as migrants in Falsterbo. Almost

**Table showing the number of migrating birds of prey at Falsterbo in the autumns of 1942, 1943, and 1944 (from Rudebeck 1950).**

| Species | 1942 | 1943 | 1944 |
|---|---|---|---|
| *Falco peregrinus* | 110 | 79 | 88 |
| *Falco subbuteo* | 4 | 3 | 12 |
| *Falco columbarius* | 156 | 215 | 156 |
| *Falco tinnunculus* | 122 | 239 | 242 |
| *Aquila chrysaetos* | 8 | 2 | 0 |
| *Aq. sp.* (non chrysaetos) | 1 | 1 | 1 |
| *Buteo lagopus* | 204 | 145 | 278 |
| *Buteo buteo* | 19 969 | 25 732 | 29 527 |
| *Buteo* or *Pernis* | 976 | 785 | 381 |
| *Pernis apivorus* | 4 633 | 1 292 | 4 571 |
| *Circus aeruginosus* | 20 | 15 | 21 |
| *Circus pygargus* | 1 | 0 | 1 |
| *Circus cyaneus* | 72 | 47 | 103 |
| *Accipiter gentilis* | 1 | 0 | 0 |
| *Accipiter nisus* | 7 136 | 7 687 | 8 231 |
| *Milvus milvus* | 58 | 57 | 63 |
| *Milvus migrans* | 1 | 0 | 1 |
| *Haliaeetus albicilla* | 7 | 12 | 8 |
| *Pandion haliaetus* | 56 | 57 | 89 |
| *Accipitres sp. ind.* | 3 | 9 | 18 |
| Total | 33 538 | 36 377 | 43 791 |

certainly this is explained by their aquatic and semiaquatic habits, respectively. They do not dislike flying over large areas of open water. *Buteo buteo, Accipiter nisus,* and *Pernis apivorus* are very strongly concentrated. The same is true for *Milvus milvus.* Within the conceivable recruiting area, this species breeds only in southern Sweden, and the number of breeding pairs hardly exceeds 50 (cf. Österlöf 1945). This means that the total number of specimens is about 200. Out of these about 60 pass Falsterbo on migration, that is, the degree of concentration is 30 %. The corresponding figure for *Buteo buteo* is probably of the same magnitude, and definitely smaller, although still high, for *Pernis apivorus* and *Accipiter nisus.* The falcons are by far not so dependent upon the guiding lines, the reason for this being their great power of flight and their readiness to fly without the aid of thermal air currents.

On the other hand there is a very close correlation between migration and weather, several species decidedly preferring "fine" weather: sunshine, good visibility, and conditions favourable for the formation of cumulus clouds. This applies particularly to those species which are most inclined for soaring, viz., *Buteo buteo, Pernis apivorus, Milvus milvus* and some others. But all these species are not equally dependent upon such weather. Thus, when weather conditions are inproving after a bad spell, *Pernis apivorus* will start on migration flight before *Buteo buteo*, the latter passing in large numbers only when weather conditions are really optimal. On such occasions, 2000—4000 or even more specimens of *Buteo buteo* can be seen in one day, the maximum number counted being 9300 (Edberg and Schölin in verbis).

As stated above, the migrating birds usually fly in a west-southwesterly direction when they leave the Falsterbo peninsula. Several times, however, I have observed that this direction will change towards the end of a good migration day. Even when weather conditions remain unchanged, the mighty stream of birds will continuously change its direction from WSW over W to WNW. The significance of this behaviour is still unknown but should be considered in relation to the experiments on directed migratory activity recently published by Kramer (1950 a, 1950 b, as well as p. 269 in this volume).

*Discussion:*

R. T. Peterson: In North America we have several migration points (Cape May, N. J., Cape Charles, Va. and Point Pelee, Ontario) which are very much like Falsterbo in Sweden. We find that most visible or low altitude migration opposes the wind — birds will not start across water unless they have an opposing wind — with an off shore tail wind birds will reverse their direction on reaching the point and will double back along the shore into the wind sometimes continuing this reverse direction for miles.

## References

KRAMER, G. 1950 a: Orientierte Zugaktivität gekäfigter Singvögel. Naturwissenschaften *37*, 1950, p. 188.

—— 1950 b: Weitere Analyse der Faktoren, welche die Zugaktivität des gekäfigten Vogels orientieren. Ibidem *37*, 1950, p. 377—378.

ÖSTERLÖF, B. 1945: Gladans (*Milvus milvus* L.) förekomst i Sverige. (With an english summary: The distribution of the Kite, *Milvus milvus* (L.), in Sweden). Vår Fågelvärld 4, 1945, p. 101—136.

RUDEBECK, G. 1950: Studies on bird migration, based on field studies in southern Sweden. Vår Fågelvärld, Supplementum 1. Lund 1950.

# Some Aspects of Bird Migration in New Zealand

*R. B. Sibson*

*Auckland, New Zealand*

The study of migration in New Zealand is concerned mainly with waders (Charadriiformes) and sea-birds (Procellariiformes and Lariformes). Twenty-one distinct arctic waders are on the New Zealand list. Of these about half arrive and depart annually at fairly regular dates. The New Zealand coast is long and observers are few; but during recent years an increase of skilled observers has shown that several arctic species which were once considered stragglers, are regular migrants and in their seasons may always be expected in certain localities. During the New Zealand summer arctic waders may be found in suitable harbours and estuaries from Parengarenga (lat 35° S) to Stewart Island (lat 47° S) and some may straggle even to the outlying subantarctic islands south of 50°. Of the indigenous waders, four species are markedly migratory. A large proportion of those which breed in the South Island winter in the northern half of the North Island.

The many small islands off the coast of New Zealand are the breeding places of several species of petrels and shearwaters. Some of these are resident; others are truly migratory and their times of coming and going are known, but much remains to be learnt about their annual wanderings which may take them into the northern hemisphere. In winter the seas of New Zealand receive a vast influx of subantarctic Procellariiformes whose movements are imperfectly understood.

No passerine birds migrate to and from New Zealand; and there is no use for trapping stations such as Ottenby, Heligoland or the Isle of May. The indigenous passerines are not adventurous fliers. Tuis (*Prosthemadera novaeseelandiae*) and Pipits (*A. novaeseelandiae*) may move down locally in winter from the high country. The many valid insular subspecies of the New Zealand passeriformes are proof that for a long period of time there has been little or no traffic between the different populations, even across such a narrow waterway as Cook Strait.

In striking contrast are the long oceanic flights made twice a year by the two migratory cuckoos. Approximate distances from North Cape to possible resting places are: Norfolk Island 450 miles, Lord Howe 750 miles, Noumea 900 miles, Fiji 1 100 miles. From the East Cape the Kermadec Islands are distant about 500 miles and Tonga about 1 400 miles.

In its remarkable flights to and from Australia the Banded Dotterel (*C. bicinctus*) has to cross the Tasman Sea which at its narrowest, between South Westland and Tasmania, is not less than 900 miles wide. There is no evidence that large numbers of migrating Banded Dotterels habitually use the shortest route nor that they call regularly at Norfolk Island or Lord Howe, both of which are rather to the north of their desired objectives.

Some of the introduced European passerines have crossed hundreds of miles of ocean to introduce themselves to remote islands, e.g. Lesser Redpoll (*Carduelis cabaret*) to Macquarie and Yellowhammer (*Emberiza citrinella*) to Lord Howe. But so far no marked seasonal movements have been noted between the North and South islands.

The ringing of birds in New Zealand is in its infancy. Small numbers of penguins and albatrosses and many silvereyes (*Zosterops lateralis*) have been marked by private individuals. In 1950 the Ornithological Society of New Zealand initiated a national ringing scheme, and the first rings stamped "send Dominion Museum, New Zealand" are now on their travels. The recovery in Western Australia of a Nellie (*Macronectes giganteus*) ringed in the South Orkney Islands and the occurrence in Ceylon of a ringed Tasmanian Muttonbird (*P. tenuirostris*) give promise of interesting results when bird-banding gets into its stride in the Southern hemisphere.

In the following summary birds have been grouped under five headings, according to the region where they breed.

1. New Zealand is the terminus for many arctic waders. Of these the most numerous are the Eastern Bar-tailed Godwit (*L. lapponica baueri*) of which it is believed that the bulk of the population reaches New Zealand and the Knot (*C. canutus*). The next commonest are Turnstone (*A. interpres*) and Pacific Golden Plover (*C. dominica fulva*).

Probably regular in small numbers are:—Sharp-tailed Sandpiper (*C. acuminata*), Pectoral Sandpiper (*C. melanotos*), Curlew Sandpiper (*C. testacea*), Eastern Little Stint (*C. minuta ruficollis*), Longbilled Curlew (*N. madagascariensis*), Whimbrel (*N. p. variegatus*). The following stragglers have been recorded 10 times or less:—Gray Plover (*C. squatarola*), Large Sand Dotterel (*C. leschenaulti*), Japanese Snipe (*Capella hardwicki*), Sanderling (*Crocethia alba*), Hudsonian Godwit (*L. l. haemastica*), Greenshank

(*T. nebularia*), Wandering Tattler (*H. incanus*), American Whimbrel (*N. p. hudsonicus*), Little Whimbrel (*N. minutus*), Gray Phalarope (*P. fulicarius*), Red-necked Phalarope (*P. lobatus*).

Many Arctic Skuas (*S. parasiticus*) habitually visit New Zealand waters and victimize the breeding colonies of *Sterna striata*; rarely troubling the Caspian Terns.

Pomarine Skuas (*S. pomarinus*) are occasionally recorded. (The Arctic Tern (*S. macrura*) has been observed only three times.) It is probable that the Needle-tailed Swift (*Chaetura caudacuta*) occurs more often than is suspected. There was an 'invasion' in 1942–1943.

Wintering (in the sense of 'staying over' for the southern winter) of Arctic waders in New Zealand: The evidence seems to indicate that these are immature non-breeders. Large numbers of Bar-tailed Godwits and Knots winter, mainly in the province of Auckland.

The following have also been recorded occasionally in winter i. e. May–August: Turnstone, Pacific Golden Plover, Sharp tailed Sandpiper, Curlew Sandpiper, Eastern Little Stint, Long-billed Curlew, Eastern Whimbrel, American Whimbrel, Gray Plover, Hudsonian Godwit, Wandering Tattler, Gray Phalarope.

2. Birds that come to New Zealand from the north to breed, arriving September-October-November and leaving March-April-May.

a) Land birds. No passerines. 2 Cuckoos, i. e. (1) *Chalcites lucidus* which migrates through Norfolk and Lord Howe Islands and to Solomons and Bismarck archipelago. (2) *Eudynamis taitensis* whose chief wintering range extends from Fiji to the Society Islands.

b) *Procellariidae*. Several species whose winter range extends to the North Pacific and the west coast of America, e. g. *P. carneipes. P. bulleri. P. griseus. P. parkinsoni. Pt. longirostris pycrofti. Pt. cooki.*

Much has yet to be learnt about their movements in winter. They are virtually unknown in the area covered by Mayr's "Birds of the S. W. Pacific." Virtually the whole population of these species leaves New Zealand.

Mottled Petrel (*Pt. inexpectata*) seems to range both south to the pack ice and also to migrate into the northern hemisphere.

Whitefaced Storm Petrel (*Pelagodroma marina*) leaves New Zealand but has not yet been recorded from S.W. Pacific (Mayr 1945).

3. Birds that breed in New Zealand and of which considerable numbers migrate W.N.W. to winter in southern and eastern Australia.

Banded Dotterel (*C. bicinctus*). Route not known. Occasional at Norfolk and Lord Howe Islands. "A quota of non-breeding birds remain in Australia during the normal nesting season" (Serventy). White-fronted Tern (*S. striata*). Numbers present in S.E. Australia May-November, apparently predominantly juveniles.

Fluttering Shearwater (*P. gavia*). Origin of Australian birds is not known, but seems to be Cook Strait.

Hutton's Shearwater (*P. huttoni*). The breeding place of this rare petrel is not yet known, but the region of Cook Strait seems to be indicated.

According to Serventy it occurs in winter in the Great Australian Bight rather to the west of the winter range of *P. gavia.*

4. Inter-island migration.

There is as yet no evidence of any passerine migration except perhaps of the Silvereye (*Zosterops lateralis*).

Wry-billed Plovers (*Anarhynchus frontalis*) entirely leave the S. I. in winter which is spent mainly on the extensive flats in the province of Auckland. The northward movement may begin about midsummer and flocks of some size are back in Auckland by mid-January.

The S. I. is almost emptied of Banded Dotterels (*C. bicinctus*) and of Stilts (*Himantopus*) in winter. Wintering flocks in Auckland increase from January-April. Southward movement begins about July.

The Banded Dotterels of the Auckland Islands, curiously enough, seem to be resident.

Of the river-bed Oystercatchers of the S. I. (*H. o. finschi*) many hundreds move north to winter in the province of Auckland; but greater numbers gather in suitable estuaries in the S. I.

Small numbers of Black-billed Gulls (*L. bulleri*) and of Black-fronted Terns (*Chlidonias albi-striata*), both river-bed nesters in the S. I. cross Cook Strait to winter mainly in Wellington province. A few *C. albistriata* reach Auckland most winters. *Sterna striata* is reported to be absent from the Chatham Islands from March to August.

5. There is a general tendency for the albatrosses, petrels and prions which breed on the subantarctic islands to move northwards in winter about to the latitude of the North Island. Observations from ships at sea are seldom made and in any case accurate sight identifications of some species are difficult or even impossible. But beachcombing for storm-wrecked birds on the long west coast of the North Island is yielding profitable results and throwing light on the northward range and migration of subantarctic breeders. After winter gales it is not unusual to find ten or more species of southerly 'tubenoses' ashore on Muriwai beach near Auckland. They may come from the subantarctic islands not only of New Zealand but

also of the Indian Ocean e. g. Kerguelen, Marion, the homes of *Pachyptila belcheri* and *Pachyptila salvini*, both of which are found as 'waifs of the storm' every winter. *P. salvini* sometimes comes ashore in such numbers as to indicate that they must be very abundant at that season in the Tasman Sea.

At least 25 species of *procellarii*-formes whose breeding grounds are to the south, have been recorded from Muriwai beach.

The southern Skua (*C. skua lonnbergi*) deserts its subantarctic breeding island in winter. Little is known of where it goes. It occasionally comes ashore near Auckland, usually when large numbers of prions are storm-wrecked.

Truly Antarctic breeding species are seldom recorded, *Fulmarus glacialoides* (about 11 records) and *Catharacta maccormicki* (3 records) have reached northern New Zealand. For Wilson's Storm Petrel (*Oceanites oceanicus*) Roberts (1940) plots only seven occurrences.

*Discussion:*

P. Scott: The occurrence of large numbers of Knots (*Calidris canutus*) and Godwits (*Limosa lapponica*) in New Zealand during their normal breeding period in the Arctic, and the fact that a partial migration occurs at this time from the South Island to the North Island, suggest that important light might be thrown on migration stimuli if specimens could be obtained and the condition of the gonads examined.

R. B. Sibson stated that the Knots were frequently in full plumage although the Godwits were in immature plumage. The relationship between plumage and development of the gonads is not apparently very close and the condition of the latter would seem to be the more significant factor. The importance of this particular example would seem to be the barrier presented by the oceanic crossing and the degree of intensity of stimulus required to force the bird across this barrier.

## References

Falla, R. A., 1937. B. A. N. Z. A. R. E. Reports (B).
Fleming, C. A., 1939. Birds of the Chatham Islands. Emu. Melbourne.
Mayr, E., 1945. Birds of the Southwest Pacific. New York.
Murphy, R. C., 1936. Oceanic Birds of South America. New York.
—— 1943–1950. New Zealand Bird Notes (now called Notornis). Masterton.
Oliver, W. & B., 1930. New Zealand Birds. Wellington.

Serventy, D. L. & Whittell, H. M., 1948. Birds of Western Australia. Perth.

1. Falla, R. A., 1936. Arctic Birds as Migrants in N. Z. Rec. Auck. Inst. Mus. 2. 3–14.
McKenzie, H. R., 1950. Records of Hudsonian Curlew in N. Z. Notornis. 4. 18–21.
Stead, E. F., 1923. Notes on Migratory Plovers of N. Z. Trans. N. Z. Inst. 54. 490–495.

2. (a) Fell, H. B., 1947. Shining Cuckoo. Trans. Roy. Soc. N. Z. 76. 504–515.
(b) Falla, R. A., 1934. Notes on breeding petrels of Northern N. Z. Rec. Auck. Mus. Inst. 1. 249–259.
Richdale, L. E., 1945. *Puffinus griseus*. Condor. 46. 1944 & 47.

3. Hindwood, K. A., 1946. *Sterna striata* in S. E. Australia. Emu. 45. 175–200.

4. Sibson, R. B., 1943. Distribution of the Wrybill in the North Island. Emu 43. 49-62.

5. Falla, R. A., 1940. The Genus Pachyptila. Emu 40. 218–236.

# Quelques aspects de la Migration d'Août en Belgique

*Alfred Van Beneden*

*Liège*

Il est établi que les mouvements de déplacement des oiseaux ne cessent pratiquement pas en Europe au cours de l'année. Tout au plus, pour la Belgique ces mouvements s'arrêtent-ils pendant la première semaine de Juin. Sitôt après, des oiseaux du pays ou des régions avoisinantes effectuent des mouvements en dehors de leur territoire de nidification ou de naissance, le plus souvent il s'agit de jeunes oiseaux affranchis, citons comme exemples, *Vanellus Vanellus* L., *Sturnus v. vulgaris* L.

En Juillet, des Anatidés, des Limicoles exécutent de plus larges mouvements erratiques ou en direction des estuaires ou des zones pourvues de nourriture, par exemple, *Ardea c. cinerea* L., *Numenius a. arquata* (L.), *Anas p. platyrhyncha* L. Les premiers Limicoles de passage fin Juillet et début d'Août sont *Tringa hypoleucos* L. et ensuite *Tringa ochropus* L., en ce qui concerne le passage à l'intérieur des terres.

Notre attention se portera particulièrement ici sur les allures de certaines espèces, lors de la migration d'Août, dans la partie Est de la Belgique dont l'altitude varie entre 150 et 500 m. et spécialement sur le Plateau de Herve.

Le début d'Août est marqué par le départ d'*Apus a. apus* (L.). *Oriolus o. oriolus* (L.), *Coturnix c. coturnix* (L.), *Lanius c. collurio* L. sont des migrateurs de ce mois, tout comme *Phoenicurus ph phoenicurus* (L.), *Sylvia c. communis* Latham, *Sylvia c. curruca* (L.) qui se groupent à certains endroits favorables. En compagnie d'oiseaux du lieu, non encore prêts pour le voyage, ils forment des associations momentanément assez denses.

*Saxicola rubetra* (L.), *Saxicola torquata hibernans* (Hartert), *Oenanthe o. oenanthe* (L.) constituent aussi des groupes migrateurs, qui vont de haies en buissons, de clôtures en champs.

*Ficedula h. hypoleuca* (Pallas), nicheurs tout à fait exceptionnels en Belgique, sont des migrateurs typiques d'Août. Du 20 Août au 15 Septembre c'est un afflux régulier d'oiseaux de cette expèce. Ils arrivent de nuit; l'observateur s'aperçoit de leur présence aux premières heures du jour.

Fin Août nous parviennent les *Muscicapa s. striata* (Pallas), venant du Nord; leur migration se poursuit pendant tout le mois de Septembre.

Nous examinerons la migration de quatre oiseaux:

*Emberiza hortulana* L., le Bruant ortolan, qui émigre du 10 Août au 13 Septembre;

*Anthus campestris campestris* (L.), le Pipit des Champs, qui émigre du 10 Août au 20 Septembre;

*Anthus t. trivialis* (L.), le Pipit des arbres, qui émigre du Ier Août au 5 Octobre;

*Motacilla f. flava* L., le Hochequeue jaune, qui émigre du 10 Août au 25 Septembre.

Ce sont évidemment des dates moyennes, ces migrateurs pouvant se présenter plus tôt et plus tard mais il s'agit le plus souvent alors d'individus isolés.

La migration de ces espèces comporte des aspects sociaux conditionnés par les affinités existant entre elles.

D'ordinaire la migration s'effectue par groupes d'individus de la même espèce mais des collectivités momentanées peuvent se constituer par le fait de rencontres dans le ciel ou au sol.

Les jeunes Bruants ortolans effectuent de courts vols erratiques dès le 15 Juillet.

Les Bruants ortolans émigrent par sujets isolés et par deux ou trois sujets. Des troupes de 4–5 sujets ne sont pas rares. Des groupements d'une douzaine de sujets sont rares; ils sont le résultat d'une accumulation nocturne d'Ortolans auprès d'un oiseau posé qui les attire par ses cris. Le même résultat peut être obtenu facilement en utilisant un oiseau captif, bon chanteur.

Les Pipits des champs sont des oiseaux peu communs en Belgique, étroitement liés à l'existence de bruyères dans des zones sabloneuses.

Les effectifs des Pipits des champs migrateurs sont composés en grande partie d'oiseaux venant du Nord. Ils ne sont jamais considérables.

On voit les Pipits des champs isolément, par couples ou en familles —5–6 individus au plus, très souvent un mâle, une femelle et des jeunes. Ils sympathisent au sol avec les *Oenanthe o. oenanthe* (L.), qui fréquentent les mêmes biotopes, les terrains sablonneux et, à défaut, les terrains rocailleux ou les chemins de terre.

Les Pipits des arbres sont communs sur toute l'étendue du territoire, pour autant qu'il y ait des groupes d'arbres à leur disposition. La migration se fait surtout par petits groupes de 4–5; à son commencement, on voit des sujets isolés, à la fin, également. Des volées d'une douzaine de sujets sont fréquentes par forte poussée migratrice.

Les Hochequeues jaunes sont des migrateurs typiques en troupes. Des sujets isolés s'observent mais ils n'ont de cesse que de rejoindre une formation de leurs congénères.

Les Bruants ortolans émigrent la nuit comme le jour. Les Pipits des champs émigrent également la nuit, on les entend dans le ciel, à forte hauteur, avant l'aube mais en pleine nuit, ils sont silencieux.

Les Pipits des arbres et les Hochequeues jaunes émigrent de jour. On les voit s'élever de leur dortoir, à l'aube.

Le passage nocturne des Bruants ortolans, surtout par clair de lune, est un fait d'observation courante. Ces oiseaux se signalent par leurs appels, le chant est peu fréquent. Les individus se répondent activement quand ils entrent en contact auditif; ils entament une sorte de conversation qui se prolonge parfois longtemps, tâchant de s'attirer mutuellement. La conversation faiblit quand ce résultat est obtenu et cesse; l'observateur peut se rendre compte du rapprochement progressif des sujets par les appels.

*Tringa hypoleucos* L. et *Tringa ochropus* L. se font entendre dans le ciel en même que le Bruant ortolan.

Si les Bruants ortolans, les Pipits des champs, les Pipits des arbres, les Hochequeues jaunes émigrent d'ordinaire, chacun pour eux, des troupes hétérogènes se forment souvent. Des Bruants ortolans se découvrent dans les volées de Pipits des arbres et de Hochequeues jaunes. Ils cheminent longuement de concert avec des vitesses de vol analogues. Les Pipits des champs sont plus individualistes mais font aussi voyage avec les trois autres oiseaux étudiés mais de préférence avec les Hochqueues jaunes.

Nous nous sommes attaché à rechercher les occasions de ces vols d'affinité:

1) le hasard des rencontres dans le ciel, à même hauteur, par ex. une troupe de Pipits des arbres dont la vitesse de vol est ralentie par la fatigue est rattrapée par des Bruants ortolans ou par des Hochequeues jaunes qui viennent de prendre leur vol.

2) la tendance grégaire des migrateurs vis-à-vis des espèces parentes.

3) les circonstances atmosphériques.

Au centre d'une zone orageuse ou au-dessus d'une zone où soufflent des vents de directions différents, se manifeste une hésitation visible chez les oiseaux précités; ils exécutent des vols d'allure giratoire. Ils éprouvent apparemment une difficulté à se dégager du lieu, ils inclinent à se grouper avec les espèces pour lesquelles ils ont de l'affinité, puis survient, semble-t-il, une détermination, ils se dirigent de concert vers le Sud.

4) La vitesse de vol est fonction de l'intensité de l'instinct migratoire. Elle provoque une sorte de brassage des espèces en vol, dont les vitesses,

si elles sont similaires, ne sont pas identiques et subissent des influences. Des associations de vol s'établissent, parfois bientôt rompues par la fatigue, la faim ou des réactions divergentes.

5) C'est la rencontre au sol qui est l'occasion la plus propice pour la formation des volées composées.

Ces rencontres au sol se produisent fortuitement mais régulièrement à la suite d'une halte dans des sites convenant aux quatre espèces, chaumes d'avoine, par ex., ou à la suite de l'arrêt pour le repos nocturne, complet ou partiel, par ex. dans des champs de betteraves qui sont les lieux les plus appropriés à déclencher l'essor de vols composés, à l'aube ou à l'aurore.

# Bird migration in NW Scania

*Torsten Malmberg*

*Zoological Institute, Lund, Sweden*

When the bird ringing method was first introduced into the study of bird migration, it was received in many countries as the only saving faith in the field of direct evidence about the migrating birds. The avifenological method fell into discredit, and perhaps it is true that the bulk of data collected by it during the latter part of the last century has not contributed so much to our knowledge of birds as to our knowledge of their observers' diligence. But, as in so many other cases in the history of science, the bird ringing method was reduced by degrees to what it really is, a most important, but by no means the only method in the hands of the student of bird migration. No wonder, therefore, that bird ringing and direct observation are now generally agreed to be complementary to each other in a rather splendid way.

During the last ten years Scanian ornithologists have devoted much time to field observations on bird migration. Scania is in many respects inviting for such studies, as many Scandinavian and Russian birds pass over a rather narrow territory here on their way to the South West. This compression of flight is of great importance especially over the Isthmus of Falsterbo in the southwesternmost part of the province. Since 1942 Rudebeck (1943) has done great pioneer work studying the autumnal migration here and has collected an enormous amount of data. In the future this will be, I think, a nearly inexhaustible source regarding the migratory habits of North European birds.

But the whole Scanian West Coast is of great interest as a gathering and guiding line for the birds directed towards the South West. Since 1944 (Malmberg 1945) I have paid special attention to bird migration conditions in North West Scania. There are still, however, only scattered observations regarding the spring migration, even though much indicates a concentration in North East Zealand (Denmark) and corresponding good obser-

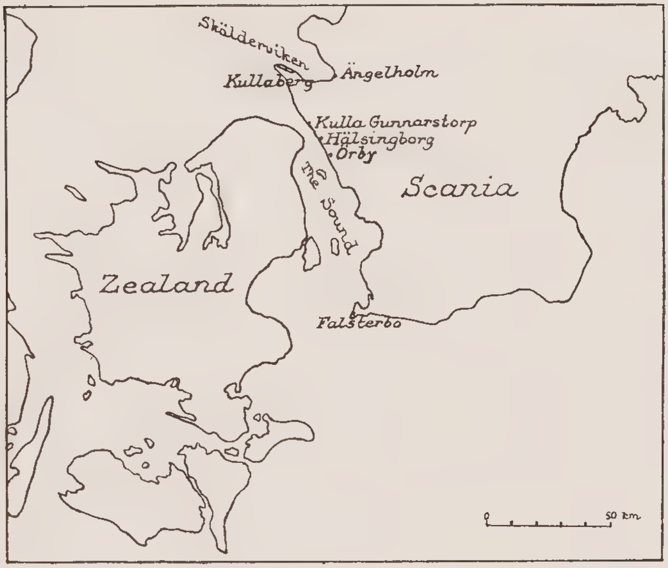


Fig. 1. Map of The Sound and adjacent territories.

vation conditions at the Kullahalvön, the pointed peninsula in North West Scania.

From the spring season I can mention the big flights of honey buzzards, *Pernis apivorus,* which regularly every year about the 1st of June come in from the sea West of Hälsingborg and often pass very low over the town, later spreading and flying over the country in a northeasterly direction. I once had a remarkably good opportunity of following this from the train to Gothenburg. Sometimes there are several hundred birds of this species passing on one day, figures that so far as I know are never noted in spring at other Scanian localities. On the whole the migration of the honey buzzard in relation to its breeding is of special interest both in spring, when my latest record is from the 21st of June, and in autumn, when the big flights pass Hälsingborg about the 1st of September (cf. Holstein 1944). During the last years good co-operation has arisen between German, Danish and Swedish workers interested in these problems (Westernhagen 1950).

Another interesting feature in spring migration here is a sometimes pronounced movement along the coast from NNW to SSE. It has nothing to do with the normal reversed migration, which can be regularly seen after sudden snowstorms and frost in the early spring, but is noted in warm and misty weather. Perhaps it is in some way related to the birds' disorientation in the mist over the sea, from which they arrive, or a tendency to cross the Swedish coast from the North West after they have followed and left the northern coast of Zealand, which might influence them to continue at least a certain distance in this false direction using the coast as a guiding line.

The autumn migration studies are mainly carried out at Hälsingborg at the most narrow part of the Sound, but observations are also made from several other localities along the coast from Örby in the south to Kullaberg Mountain in the north. Even though these investigations, to which several amateur ornithologists have contributed, are not yet finished, I think that they might nevertheless be of interest, at least for comparison with those at Falsterbo. Especially as the migration conditions are quite different at Hälsingborg from those at Falsterbo. There the migrating birds are crowding over a narrow isthmus, as long as possible—in most cases at least—avoiding the sea. Here there is a coastline running from NNW to SSE, at which the migrating birds arrive and most often follow as a guiding line, but which never can compress them in the same way as the Isthmus of Falsterbo.

That a marked concentration is noticed a little north of Hälsingborg is, of course, partly due to the fact that the distance to Denmark is only about 4 km here, but probably mainly to another thing. Most of the birds, which have followed the Swedish West Coast, will namely reach the Sound at that point after having traversed the two Northwestern Scanian peninsulas.

It is in fact astonishing, that in normal cases only a few birds leave the coast here and continue to Denmark in their normal migration direction, which most of them consequently change to a SSE one. When the coast line is nearly straight as here, the birds are evidently more inclined to take a somewhat "false" direction than to cross even a 4 km broad sound with the land on the other side very clearly visible. Probably their reaction is different, when they arrive at the capes a little more to the south. In any case I do not think that the birds seen at Hälsingborg ever reach Falsterbo, but the most narrow part of the Sound is not used as a point of departure from Scandinavia to such an extent as might be expected. Among the species which, however, often prefer to leave here are many waders, above all the strongly West-orientated lapwing, *Vanellus vanellus*, and common curlew, *Numenius arquata*, further many corvines and birds of prey. Also small groups of passerines normally leave, and on very good flight days there can be a stream of chaffinches, *Fringilla coelebs*, flying over to Denmark as far north as can be seen. On such a day, the 19th of September 1945, I counted over 16 000 specimens passing over me during 3 1/2 hours, in spite of unceasing rain.

Speaking of chaffinches, I cannot neglect to mention an observation made at the end of May in 1949 on the Kullaberg Mountain. At the outmost point of the peninsula I saw small groups of chaffinches uttering their normal call notes of migration passing over their numerous singing fellows toward the West. I cannot find any other explanation for this phenomenon than that it must have been supernumerary or in any case non-breeding birds, which, driven by some remaining migration instinct, returned at this early date. Perhaps such a late-spring movement in the autumnal direction is a rather normal thing in several species. It is, however, very seldom observed because of the extreme fewness in number of the participants and because of the fact that attention is never fixed upon such things at that time of the year, if the birds are not concentrated a little as might be expected at the westernmost point of a peninsula.

Of course, it is impossible in these few minutes to give even a short survey of recent problems and conditions of bird migration in North West Scania, not to speak of the different species observed. The methods used in noticing the data, species, number, direction, height, general behaviour, influence of weather and so on, are on the whole the same as at Falsterbo and Ottenby and will not be dealt with here. I shall only name that the observation terms are very extensive and continuous especially in the morning hours.

In general the same main species occur at Hälsingborg as at Falsterbo, but the first flocks of the season arrive, as might be expected, in several species a little earlier at the northern than at the southern parts of the Sound. Mostly steady western and north-western winds make their flight more and more sparse at Hälsingborg, but good at Falsterbo, evidently because the birds passing over Scania are driven towards the eastern and southern coast lines. Eastern and southeastern winds have the opposite effect and are accompanied by a very good flight at Hälsingborg, if I might be allowed to give such a rough sketch of the very complicated relations between bird flight and wind.

A comparison of the total numbers of species and birds passing at Falsterbo and at Hälsingborg gives, of course, much lower figures for the latter place. Especially waders and ducks but also birds of prey are generally rather sparse at Hälsingborg, most probably at least partly because these birds will take a more direct western route from their halting-places in the Bay of Skälderviken, respectively the woodlands at Ängelholm and Kulla Gunnarstorp. Comparatively high figures are obtained for many passerines, corvines and pigeons, of which latter species several thousand specimens a day can pass. However, I have never seen any counterpart in my research area to the remarkable "summer flight" (Zwischenzug) of the stockdove, *Columba oenas*, at Falsterbo.

There are, in fact, good opportunities for studying some very interesting features of migration behaviour at Hälsingborg, e. g. when a flock of lapwings directed West influences a flock of starlings, *Sturnus vulgaris*, passing at the same time along the coast towards SSE, to change direction and circle out over the sea, until the two flocks disappear to the West, the starlings thus apparently "induced" to take another way than the previous one. I cannot yet find any explanation at all for many of the migration features observed, among others the behaviour of the migrating swallows, *Hirundo rustica*, which at my observation place a little north of Hälsingborg, seem to go out over the sea in late summer every afternoon just towards the setting sun, thus changing direction from South to Northwest, evidently in some way influenced by the sun. Perhaps Gustav Kramer's recent investigations can contribute to the understanding of these phenomena.

The number of passing birds may be great or small, there is never any lack of problems for the student of bird migration.

## References

Holstein, V., 1944. Hvepsevaagen *Pernis apivorus apivorus* (L.). Biologiske studier over danske rovfugle 2. København.

Malmberg, T., 1945. Iakttagelser över flyttfågelsträcket vid Hälsingborg. Fauna och Flora 40: 207–216.

Rudebeck, G., 1943. Preliminär redogörelse för fågeliakttagelser i Skanör och Falsterbo hösten 1942 (Zusammenfassung). Vår Fågelvärld 2: 1–58, 65–88.

Westernhagen, W. von, 1950. Der Zug des Wespenbussards (*Pernis apivorus* L.) zwischen Skandinavien und Nordwest-Deutschland. Ornithologische Berichte 2: 69–84.

# Swift (Apus apus L.) Movements in Summer

Ottenby Bird Station Report No. 10

*Gunnar Svärdson*

*Institute of Freshwater Research, Drottningholm, Sweden*

Ottenby Bird Station, situated on the southernmost point of Öland in the Baltic, gives very favourable possibilities for the study of swift movements. No swifts are breeding there and practically all swifts observed are moving birds, apart from a few which breed in a small village 5 kilometers from the point.

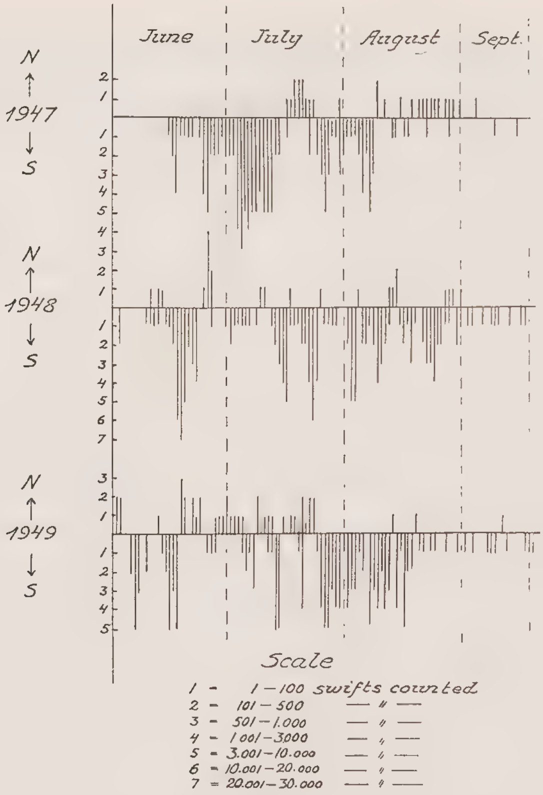
At Ottenby all passing birds are counted during the entire day. Furthermore this activity lasts from the beginning of June to November 1st.

During the season passing swifts are seen almost every day. In the years 1947–1949 the July-months have provided 93 observation days, on which passing swifts have been observed and noted on 87 days. That means only two July-days per annum were free from moving swifts.

The details of three years' study of swift movements are given in figure 1. The number of swifts counted has been roughly grouped in a 7-degree scale, where the highest figure means that between 20 000 and 30 000 swifts have been seen passing the station during the day. North- and south-flying birds have been marked by different lines drawn up or down from the zero-axis.

The great majority is always flying south, i. a. WSW-S-ESE, irrespective of season. This most probably depends on the fact that the isle of Öland serves as a guiding line for south-moving birds only. It may also be possible that north-moving birds on the average fly in better weather when they might move higher, out of sight from the ground.

It is a remarkable fact that north- as well as south-moving birds may be observed in every month. It may be added here that thousands of swifts have been noted on south-flight in May 1950. As can be easily seen from the diagram there is no obvious concentration of days when the birds fly north in spring or south in autumn. So we must conclude that the movement called "ordinary migration" is not recorded for swifts on the south point of Öland, though that of other birds are.



Note: In 1947 the observations started June 15th.

Fig. 1. The passage at Ottenby Bird Station of swifts during three summers.

Quite recently the Finnish ornithologist Koskimies has pointed out in a comprehensive paper that the swift flights in high summer are no true migration but weather-flight movements. By these movements the birds avoid the unfavourable weather of a cyclone. This leads to a transfer of birds to regions with a better food supply. According to Koskimies (Koskimies 1950) the birds fly around the cyclone by means of the typical swift reaction to fly against the wind.

From the field books of Ottenby Bird Station 1947–1949 all days with more than one thousand moving swifts have been extracted and submitted to a weather map analysis. Such "top-days" have occured 11 times in June, 24 times in July and 12 times in August. All but one concern south-moving birds.

The analysis has shown that all but 4 of these "top-days" occurred during the passage of a cyclone over the Baltic area. In the great majority of cases strong flights of swifts have been seen at Ottenby the day after heavy rainfall on the Swedish mainland. In some cases, however, the rain has fallen over southern Finland or the east coast of the Baltic. The correlation between rainfall and swift flights seems to be quite certain.

The remaining 4 top-days were all of very moderate magnitude and all came in the first week of August. These swift-movements might thus have been caused by some other agent than the weather, i. a. by spontaneous migration to the south in the autumn. It is known that most swifts disappear from their breeding places in Sweden during the first week of August.

The 39 top-days, which must be ranked as weather-flights, thus in the main confirm that at Ottenby practically all swift movements are weather-reactions, by means of which the birds fly away from an area, where their feeding is hampered. Since the great majority of the cyclones move NE this means that swifts on the Swedish mainland will often first experience a SE-wind at the front of the cyclone, i. a. when the wind increases and the sky is progressively more clouded and rain begins to fall. In this way, supposing they fly against the wind, as is always seen in the field, a lot of swifts will accumulate on the Baltic coast, moving south along it. Also when the wind is turning SW or W they are still seen following the coast of Öland southwards. Perhaps the coast will act as an important guiding line. But they may also come from south Finland or the east coast of the Baltic, going right over the sea. A very instructive, though unusual, case was observed 25. 6. 48, when more than one thousand swifts were passing northwards at Ottenby; the only top-day of this kind so far recorded. A cyclone over Poland caused rain over the southeast corner of the Baltic and the land area of Poland. The cyclone moved, as is very seldom the case, NW out over the Baltic and a strong NW-wind was blowing at Ottenby. The swifts were again driven in front of the cyclone and passed Ottenby before the rain began to fall.

The swift observations at Ottenby thus strikingly confirm Koskimies's statements (op. cit.), but indicate that weather-flights do occur during the whole summer and not only in high summer as stated by him.

Several questions arise regarding the swifts movements, i. a.

i) is the normal wandering of swifts from Europe to Africa built up by a number of separate weather-flights or is it only in summer the bird displays this striking mobility?

ii) What birds participate in the summer weather-flights? Only immature birds from last summer or breeding birds too?

Regarding the first question some evidence may come from the observations of swift behaviour in the breeding territories when a sudden rain occurs. In the Stockholm area I have seen the swifts aggregate very rapidly to flocks of 80 or more, all flying together against the rain and wind until they disappear. Even if this was only a very local flight, it indicates that the swift has instinctive reactions which are released by "bad" weather. This may indicate that weather flights occur throughout the year. In the Belgian Congo, enormous flocks of swifts have been seen in connection with the passing of tropical cyclones (A. de Bart, pers. communication) which also speaks in favour of weather-flights. Finally, in the last half of October, occassional swifts have occurred in southern Sweden in connection with northern winds. In one case a bird was observed at Ottenby flying in from the sea going northwards.

Koskimies (op. cit.) assumes that mainly immature birds participate in the summer weather-flights. This may be true but, sometimes at least, breeding birds probably take part as well. In July 1947 a lot of breeding swifts disappeared from their nests at Hasselfors in middle Sweden (Magnusson and Svärdson 1948) and an enormous passage was noted at Ottenby. When the movement assumes greater dimensions, caused by long periods of bad weather, breeding birds probably move as well. In 1947 more than 400 passing swifts were ringed at Ottenby and in the two consecutive summers 6 were reported from probable breeding areas. They came from middle Sweden and Norway (from Stockholm to Kongsvinger) which means that a bad weather escape may be a flight of roughly 1 000 to 2 000 kilometers, until they are back home again.

## References

Koskimies, J., 1950. The life of the swift, *Micropus apus* (L.), in relation to the weather. Ann. Acad. Scient. Fenn. Ser. A: 1–151.

Magnusson, M. & Svärdson, G., 1948. Livslängd hos tornsvalor (*Micropus apus* L.). Age of Swifts. Vår Fågelvärld 7: 129–144.

# Migration to North Norway of Barnacle Geese which had been bred in Scotland

*John Berry*

*Edinburgh*

The Barnacle Goose, *Branta leucopsis* (Bechst.) is plentiful locally on the west coast of Scotland, but it is seldom met with on the east coast. On the Firth of Tay in East Scotland, a winter resort of other wildfowl, there appears to have been no record before 1948 of a flock of Barnacle Geese having been seen numbering more than about half a dozen individuals. Most of the records were of single birds noted late in the winter.

At Tayfield, Newport-Fife, on the Firth of Tay (about 56°26′ N., 2°56′ W.) full-winged Barnacle Geese have nested in a semi-wild state for more than ten years. On 6th March, 1948, two stray dogs got into the field where the geese usually live throughout the year. The dogs killed some geese and others flew away. Twenty-one full-winged Barnacles disappeared. There was thick fog at the time and throughout the next day, which may have prevented the Barnacles finding their way back.

On 15th March, 1948, one of the Tayfield Barnacles was shot on a farm in Narøy Komune, Nord Trøndelag, Norway (about 64°50′ N., 11°20′ E.,) Another was shot near Alstahaug, Norland (about 66°N., 12°50′ E.) on 20th March. On 31st March, ringed Barnacle Geese were reported near Skrolsvik, in Senja, (about 69°05′ N., 17° E.) and were so tame that they took food thrown to them. Two were caught on 8th April. They were Tayfield geese. One of those caught near Skrolsvik and released was recaptured on 16th May in the Barentz Sea (about 72°26′ N., 37° E.). Other reports from Norway told of ringed Barnacle Geese, seen but not captured, at Glein near Sandnessjøen and at Søroffersøy in the same district, about 30th April.

On 1st June, 1948, it was found that five of the missing Barnacle Geese had returned to Tayfield, in East Scotland, where they were then nesting.

In the first week of October, 1948, a flock of eight Barnacles, four of them thought to be young birds, arrived on the Firth of Tay; later four more were seen and these twelve geese spent the whole winter there.

In October 1949 about twenty-five Barnacle Geese came to the Tay. The

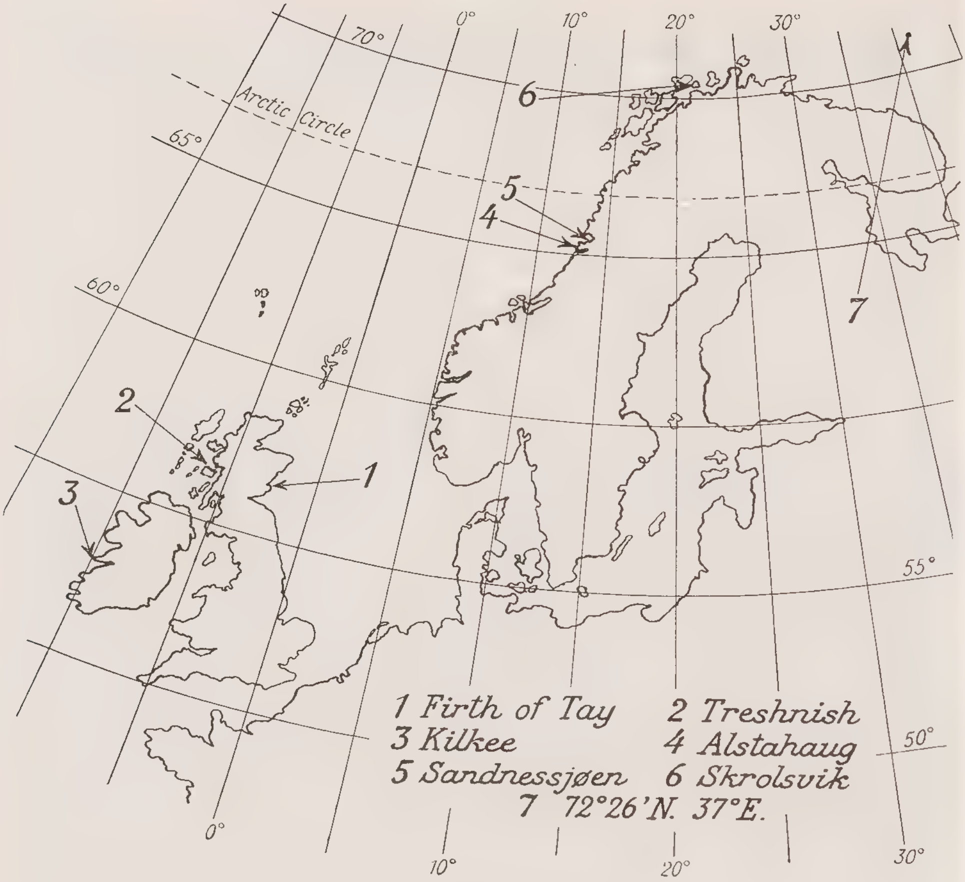


Fig. 1. Explanation in text.

species is given legal protection throughout the whole year on that Firth, so that reports of ringed birds were not to be expected. But on 30th January 1950, one of the flock (still numbering about twenty-five) was shot in error by a wildfowler. It was one of the ringed geese which had disappeared from Tayfield on 6th March, 1948, and almost certainly was one of those which had migrated to North Norway.

It may be just possible that the survivors of the Tayfield Barnacle Geese which went to Norway have established a new breeding colony from which they are beginning to make regular migrations to spend winter on the Firth of Tay in East Scotland. Any reports of Barnacle Geese being seen in summer, or on migration, in new haunts in North Norway would therefore be particularly interesting.

# Les Cigognes blanches de l'Afriqe du Nord et leurs Migrations

*G. Bouet*

*Paris*

A l'occasion du Congrès d'Oxford en 1934, j'ai attiré l'attention sur l'intêret que présentait le problème, à peu près totalement inabordé jusqu'alors, de la migration des Cigognes blanches *Ciconia ciconia ciconia* (L.) de l'Afrique du Nord (Bouet 1938 a). Je signalais en même temps la première campagne de baguage des Cigognes au nid, entreprise par mes soins au cours du mois de Juin de la même année en Algérie, où j'avais pu baguer une cinquantaine de jeunes Oiseaux.

Par la suite, de telles campagnes de baguages ont été renouvelées chaque année dans cette région et leurs résultats exposés en diverses publications, dont une synthèse a été présentée par moi au Congrès de Rouen en 1938.

Quelles acquisitions nouvelles sur la biologie des Cigognes nord-africaines avons-nous réalisées depuis lors, c'est à dire depuis plus de dix ans?

Je rappelerai tout d'abord qu'au cours des années 1938, 1939, 1940 et 1941, les campagnes de baguage furent continuées. En 1942, 1943 et 1944, il ne fut pas possible de faire parvenir en Algérie le matériel nécessaire par suite de la guerre. En 1945 les opérations de baguage furent reprises et n'ont pas cessé depuis cette date. En voici le résumé:

En 1938 462 baguages furent effectués; en 1939 299; en 1940 275; en 1941 275 également. Après la guerre nous avons du supprimer le centre de Bône par suite de difficultés de baguage locales. En 1945 200 bagues furent posées; en 1946 200; en 1947 225; en 1948 275 et enfin en 1949 375.

En résumé le chiffre total des baguages effectués en Algérie de 1938 à 1949 est de 2 586. Si on y joint celui obtenu de 1934 à 1937 soit 1 624, on arrive à un total de 4 210 baguages. Quelles ont été pendant cette même période les reprises de bagues sur des Cigognes nord-africaines parvenues à notre connaissance? Elles sont peu nombreuses. En voici le résumé:

| | | | |
|---|---|---|---|
| 1938 | B 5204 | Cerez Juin (Bordj bou Arreridj) ... | Sfax 1938 sans date (Tunisie) |
| 1938 | B 5369 | Mirabeau Juin (Alger) ............ | Laghouat Juillet 1939 (Territoires du Sud) |
| 1938 | B 5597 | Relizane Juin (Oran) ............. | Relizane fin Janvier 1939 (Oran) |
| 1938 | B 5204 | Cerez Juin (Bordj bou Arreridj) ... | Gorges de Seldja près Metlaoui (Tunisie)! Avril |
| 1939 | B 3919 | Tamara Juin (Maroc)............. | Nguru 400 Kil; Ouest! 1939 du Tchad Oct. 1939 |

| | | | |
|---|---|---|---|
| 1939 | B 6864 | Mirabeau Juin | Ippy Avril 1940 (Oubangui-Chari) |
| 1939 | B 6887 | Mirabeau Juin | Palmeraie de Sidi Yahia près de Djaama Avril 1940 (Algérie) |
| 1940 | B 7317 | Mirabeau Juin | Congo belge sans indication de localité mais antérieurement à Oct. 1948 |
| 1940 | B 6723 | Bordj bou Arreridj Juin | Ntungamo — Rumpara — Ankolz (Ouganda) Mars 1941 |
| 1946 | B 8433 | Relizane Juin | Toufana près Batna Avril 1947 (Constantine) |
| 1946 | B 8467 | Mirabeau Juin | Misterblance près Catane (Sicile) Mai 1947 |
| 1947 | B 9338 | Davoust Juin (Bordj bou Arreridj) | Mizda (Frontière du Fezzan 150 Kil. sud Tripoli Juin 1948 |
| 1947 | B 8584 | Mirabeau Juin | Région de Mateur Avril 1948 (Tunisie) |

Si ces reprises de bagues ne nous ont apporté que peu de précisions nouvelles sur les routes de migration suivies par les Cigognes nord-africaines se dirigeant vers le Centre Afrique, nous avons par contre obtenu de nouvelles données sur l'une des routes suivies par les Oiseaux: Rousselot, vétérinaire en service en Afrique occidentale (1941) a montré que dans le Cercle de Tanout entre Niamey et Zinder des vols de Cigognes atteignant parfois plusieure milliers sont signalés chaque année en Novembre-Décembre et il les a lui-même observés. Le même observateur au cours de tournées plus à l'Ouest vers Mopti sur le Niger a vu un vol d'une cinquantaine et un de mes correspondants m'a signalé la rencontre qu'il fit en Décembre 1938 de milliers de Cigognes perchées par groupes de 5 à 6 sur des épineux à une trentaine de Kil. de Hombori, sur la route allant à Gao. En 1943, c'est un observateur anglais qui, à la hauteur de Niafunké, puis au lac Faguibine, au sud de Tombouctou, compte un groupe d'une cinquantaine et au Faguibine de larges vols planant au dessus du lac (Guichard, 1947). Si nous nous en rapportons aux observations de R. Malbrant (1949) au Tchad, nous voyons que chaque année de nombreuses bandes sont signalées dans les deux Territoires du Tehad et de l'Oubangui en Novembre et Décembre. La plupart de ces bandes suivent le cours du Chari et disparaissent. Cependant un certain nombre d'Oiseaux semblent passer la plus grande partie de l'année dans certains marais (Lac Fittri). Il s'agit vraisemblablement de jeunes Cigognes «érratiques» qui «vagabondent» à travers l'Afrique en attendant leur maturité sexuelle.

Malbrant nous donne un tableau des reprises faites au Tchad et dans l'Oubangui. Malheureusement, pour un certain nombre d'Oiseaux en provenance de Rossitten (Prusse orientale), nous ignorons les dates de baguage. Sur un total de 14 reprises, 3 proviennent de Cigognes nord-africaines qui ont été capturées à Ippy (Oubangui-Chari), au Congo belge et à 400 Kil. à l'Ouest du lac Tchad (peut-être en Nigeria?). Ces reprises, en ce qui concerne les Oiseaux nord-africains, complètent en la rendant certaine l'hypotèse des routes de migration s'étendant en évantail depuis le sud du Sahara jusqu'au Centre Afrique et vers l'Ouganda. Les reprises d'Oiseaux nordiques montrent qu'un certain nombre de ces Cigognes traversent du nord au sud l'Ouadaï ou viennent échouer dans l'Oubangui-Chari. Il semble d'autre part résulter des observations de Chapin et de Malbrant que la grande Forêt Hygrophile du Congo belge et du Gabon aussi bien que du Cameroun est une barrière infranchissable pour le Cigogne blanche qui obliquerait vers l'Est dès qu'elle arrive au contact de la grande Forêt.

Avant de clore cet exposé, je dois signaler une observation portée à ma connaissance par la Mairie de Mirabeau (Alger). Au début du printemps de 1948, au moment de la migration d'arrivée des Cigognes dans cette localité, deux Oiseaux — au moins — ont été aperçus munis d'une bague à la patte. Ils sont restés tout l'été sur le territoire de la Commune et ont niché. Aucun renseignement plus précis ne nous a été fourni. Au printemps de 1949 la présence des mêmes (?) Cigognes baguées a été confirmée. De nouveau ces Oiseaux auraient niché.

Il s'agit vraisemblablement de jeunes Cigognes nées et baguées antérieurement à Mirabeau; mais nous ne pourrons obtenir de précisions sur leur identité qu'en sacrifiant une des porteuses de bague, ce que jusqu'ici nous avons évité de faire.

Telles sont les observations que nous avons faites sur la biologie des Cigognes nord-africaines depuis 1938.

## Références

Bouet, G., 1936. Nouvelles recherches sur les Cigognes blanches d'Algérie. L'Oiseau et la Rev. franç. d'Ornithol. No. 2: 300.

—— 1938 a. Le problème de la migration des Cigognes blanches (Ciconia ciconia ciconia L.) de l'Afrique du Nord. Proc. VIIIth Int. Ornithol. Congress, Oxford 1934: 671.

—— 1938 b. Nouvelles recherches sur les Cigognes blanches de l'Afrique du Nord. L'Oiseau et la Rev. franç. d'Ornithol. No. 1.

Bouet, G., 1938 c. Baguages de Cicognes blanches dans l'Afrique du Nord. Bull. Mus. Hist. Nat., Paris, 2$^{me}$ Série, 10.

—— 1940. Le problème de la migration des Cigognes blanches de l'Afrique du Nord. Compte rendu sommaire des Séances de la Soc. de Biogéographie 17, No. 143.

—— 1950. La vie des Cigognes. Paris.

Guichard, K. M., 1947. Birds of the Inundation zone of the River Niger, French Soudan. Ibis 89: 450–489.

Malbrant, R., 1949. Les migrations de la Cigogne blanche en Afrique Equatoriale française. L'Oiseau et la Rev. franç. d'Ornithol. Nelle Série 19, No. 2.

Rousselot, R., 1941. Migrations des Cigognes nord-africaines. L'Oiseau et la Rev. franç. d'Ornithol. Nelle Série 11, No. 1.

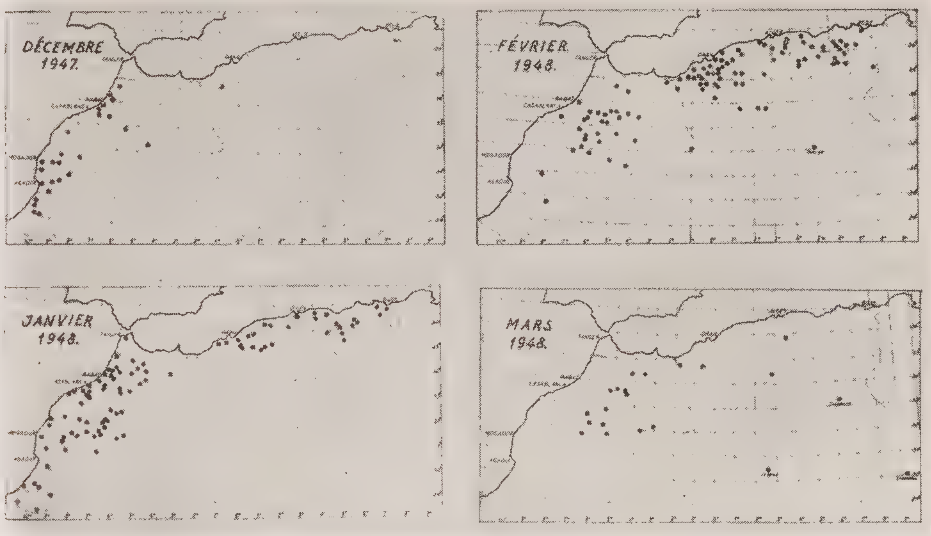
# Contribution à la Connaissance de la Migration des Cigognes Blanches (Ciconia ciconia (L.)) en Afrique du Nord

*Poul Jespersen*

*Copenhague*

Pendant un séjour à Alger en 1947 j'ai appris que l'Institut de Météorologie et de Physique du Globe de l'Algérie possedait des materiaux d'observations sur l'arrivée de la Cigogne Blanche en Algérie. Grâce à l'aimable permission du directeur de l'Institut j'eus l'occassion lors de mon séjour à Alger d'examiner la grande collection des formulaires météorologiques et d'en extraire toutes les dates d'observations des Cigognes. J'ai traité les materiaux de 15 années, c'est-à-dire de 1928 jusqu'à 1942. Une note sur mes travaux est publiée dans le Bull. Soc. Hist. Nat. Afrique du Nord, volume 40, no. 6, p. 138–160 (1950), mais elle donne seulement les observations des régions les plus septentrionales de l'Algérie.

Pour suivre mes observations sur l'arrivée de la Cigogne dans une plus grande région j'ai obtenu en 1948 des materiaux sur les dates d'arrivées des Cigognes non seulement d'Algérie mais aussi du Maroc. Les observations se rapportent à l'hiver 1947–48 et au printemps 1948. Les materiaux sont dû à l'aimable assistance, partiellement de l'Institut de Météorologie de l'Algérie et partiellement de l'Institut Scientifique Chérifien. Les renseignements de l'Algérie viennent des observateurs météorologiques — en particulier grâce à mon ami Monsieur J. Dubief, Alger. Au Maroc un questionnaire fut envoyé aux autorités administratives du Protectorat, au personnel des Eaux et Forêts et encore à celui de l'Instruction publique. D'autres renseignements furent demandés directement au personnel des Stations météorologiques. Les materiaux du Maroc m'ont été envoyé par M. Jean B. Panouse de Rabat. Ce sont des materiaux déjà employés pour une note de M. Panouse "Les migrations des Cigognes marocaines," qui va paraître bientôt dans le Bulletin de la Société des Sciences Naturelles du Maroc. Les renseignements sont rassemblés sur mon initiative de l'Institut Scientifique Chérifien, et je remercie M. Panouse des cartes, qui me furent envoyées et sur lesquelles les observations avaient été enregistrées.



DÉCEMBRE 1947.

FÉVRIER 1948.

JANVIER 1948.

MARS 1948.

Fig. 1. Observations de Cigognes en Algérie et au Maroc en décembre 1947 et en janvier, février et mars 1948.

Dans la figure 1 les points noirs montrent les places où les Cigognes furent observées pour la première fois en Algérie et au Maroc en décembre 1947, en janvier et février 1948 et au mois de mars 1948. On voit qu'il y a un bien plus grand nombre d'observations au Maroc en décembre 1947 qu'en Algérie. Il y a seulement deux observations de l'Algérie, mais un assez grand nombre d'observations du Maroc, c'est-à-dire que la Cigogne arrive considérablement plus tôt au Maroc qu'en Algérie. Par contre nous avons beaucoup d'observations en janvier et février en Algérie ainsi qu'au Maroc. Au mois de mars on relève encore beaucoup d'observations au Maroc, mais relativement peu en Algérie.

En comparant les observations du Maroc pour les différents mois on remarque ce résultat intéressant, que les premières observations—c'est-à-dire celles de décembre et janvier — sont presque toutes dispersées dans le voisinage de la côte atlantique, mais que celles de février et de mars sont généralement relevées plus à l'interieur du pays. Ici il faut remarquer le fait, que la Cigogne arrive notablement plus tôt au Maroc qu'en Algérie et au Maroc elle arrive évidemment plus tôt dans les régions assez proches de la côte atlantique.

Nous allons maintenant étudier l'arrivée de la Cigogne dans la région proprement dite — saharienne.

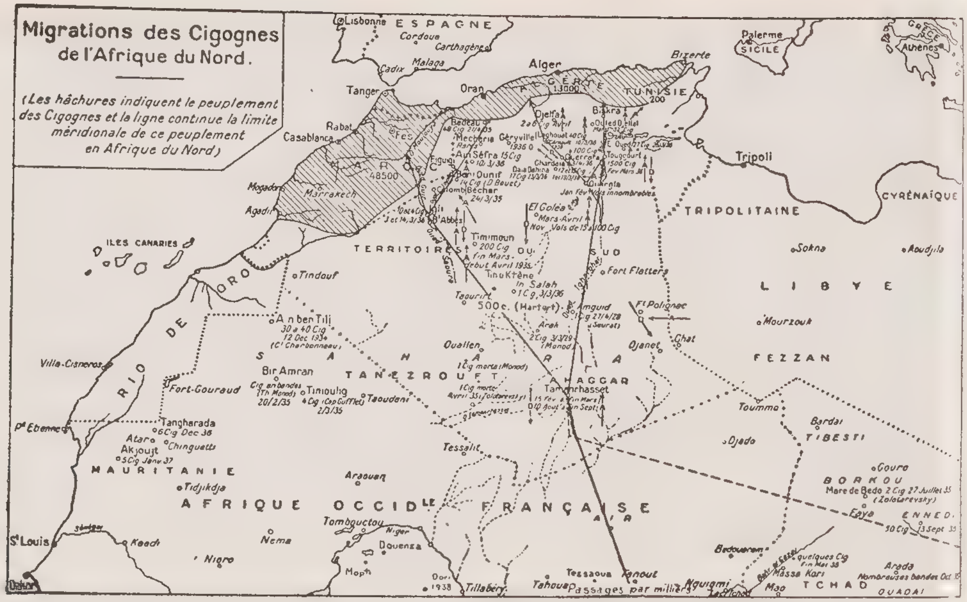


Fig. 2. Migrations des Cigognes de l'Afrique du Nord d'après G. Bouet (1950).

La figure 2 montre une carte élaborée par M. le docteur G. Bouet, Paris. Le docteur Bouet a grand mérite d'avoir rassemblé toutes les observations sur la migration de la Cigogne en Afrique du Nord. Il montre dans cette carte des routes spéciales de la migration d'après les renseignements qu'il avait en main. Les recherches de M. Bouet (1938, 1950) donnent le résultat, que la Cigogne suit une route du sud jusqu'au Haggar. Là se produit une première division des migrateurs. Les uns se dirigent plein nord (route du Nord) et arrivent à Ouargla et de là peuplent une grande partie de l'Algérie et de la Tunisie. Les autres s'orientant plus à l'ouest jusqu'à Béni Abbès (route de l'Ouest). Là encore, selon le docteur Bouet, les oiseaux se séparent en deux groupes: le premier va nicher dans l'Oranais tandis que le second atteint le Maroc. — Selon les renseignements obtenus il y a cependant du doute à propos de la route des Cigognes du Maroc et de leur passage au Haggar.

Voici d'abord une carte (figure 3) qui donne les noms des localités où les Cigognes sont observées en hiver et au printemps dans le Sahara proprement dit. On voit que les places d'observations se rassemblent en deux grands groupes séparés par un vaste intervalle sans observations ce qui est sûrement du au manque d'observateurs. La région d'ouest s'étend de Legroniat au sud jusqu'au Tindouf au nord, la région d'est de Tamanrasset (Haggar) au sud jusqu'à Colomb Béchar et Touggourt au nord.

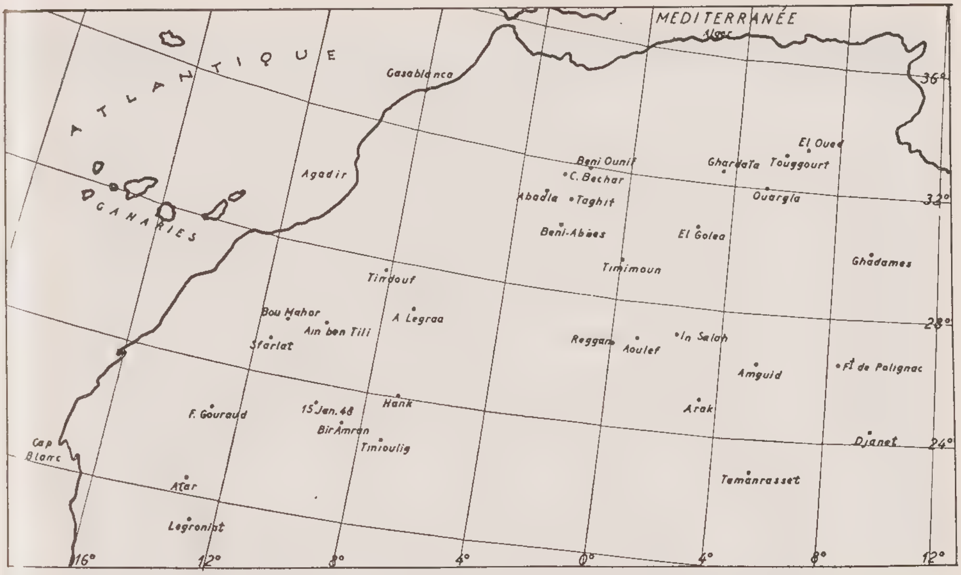


Fig. 3. Les noms des localités où les Cigognes sont observées en hiver et au printemps dans le Sahara.

Les quatre cartes de la figure 4 présentent les régions du Sahara même, où l'on a observé les Cigognes pendant les quatres périodes suivantes: décembre, janvier, février et mars/avril. Chaque point donne une date où l'on a observé des Cigognes en migration en hiver et au printemps. Une localité avec trois points, par example, montre ainsi qu'il y fut observé des Cigognes à trois différentes dates. Les observations datant de différentes années sont basées d'une part sur les renseignements de la litterature, d'autre part sur les observations non encore publiées.

Regardons premièrement la carte de décembre. Toutes les observations se trouvent dans la région occidentale et il n'y a pas d'observations de Haggar (Tamanrasset). Cela montre que les premières Cigognes de passage se trouvent dans la région plus ouest du Sahara. Cela correspond bien avec la constatation que la Cigogne arrive plus tôt au Maroc qu'en Algérie. Il s'agit donc vraisemblablement d'oiseaux qui sont en route vers le Maroc. En janvier il y a aussi des observations de la région occidentale du Sahara. Cependant on relève quelques observations de Tamanrasset et d'autres répandues sur la région orientale du Sahara. Néanmoins ce n'est qu'à partir du commencement de février que nous avons un grand nombre d'observations de Tamanrasset, ainsi que de plusieurs localités dans la région orien-

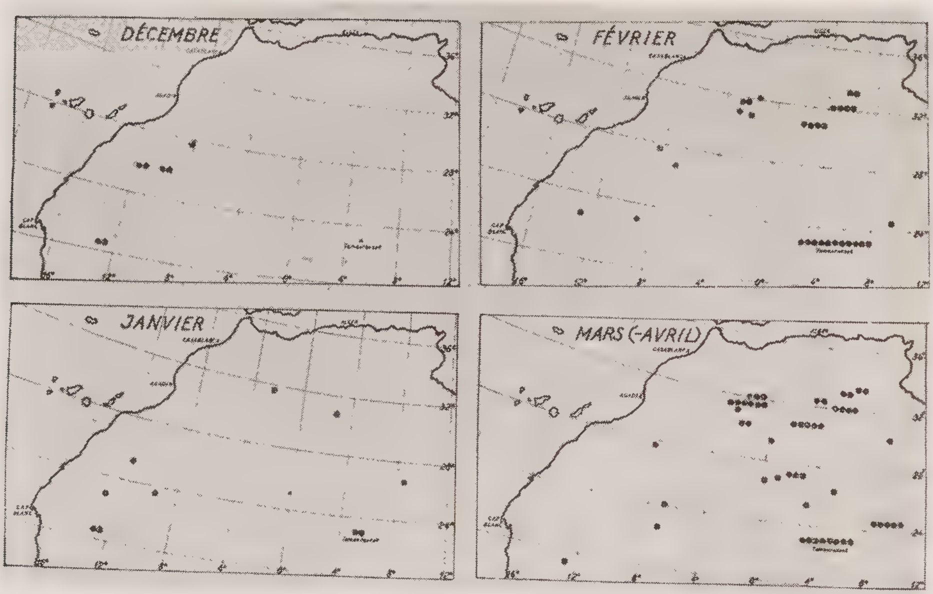


Fig. 4. Observations de Cigognes dans le Sahara en hiver et au printemps (voir le texte).

tale. Enfin, aux mois de mars/avril il y a un grand nombre d'observations de Tamanrasset ainsi que de certaines régions orientales. Nous avons pourtant aussi quelques observations de la région occidentale.

Ces cartes montrent assez clairement que les observations de migration les premières en date (c'est-à-dire en décembre) viennent seulement de la région occidentale; quant au passage sur Tamanrasset et la région orientale il ne commence que plus tard, c'est-à-dire en janvier-février. — Cela montre à mon avis que les Cigognes du Maroc, qui arrivent en grand nombre déjà en décembre, ne peuvent pas passer par Tamanrasset, mais doivent faire un trajet bien plus occidental et vraisemblablement aussi passer plus au sud.

Ce n'est pas toujours qu'on reçoit des renseignements sur le nombre de Cigognes observées. Dans plusieurs cas il y a pourtant les renseignements approximatifs quant au nombre d'oiseaux observés. La carte de la figure 5 présente une impression de la quantité de Cigognes observées dans les différentes localités.

Nous avons dans la région orientale un nombre extrêmement grand qui donne près de Tamanrasset jusqu'à mille (une seule fois, le 16 février 1947,

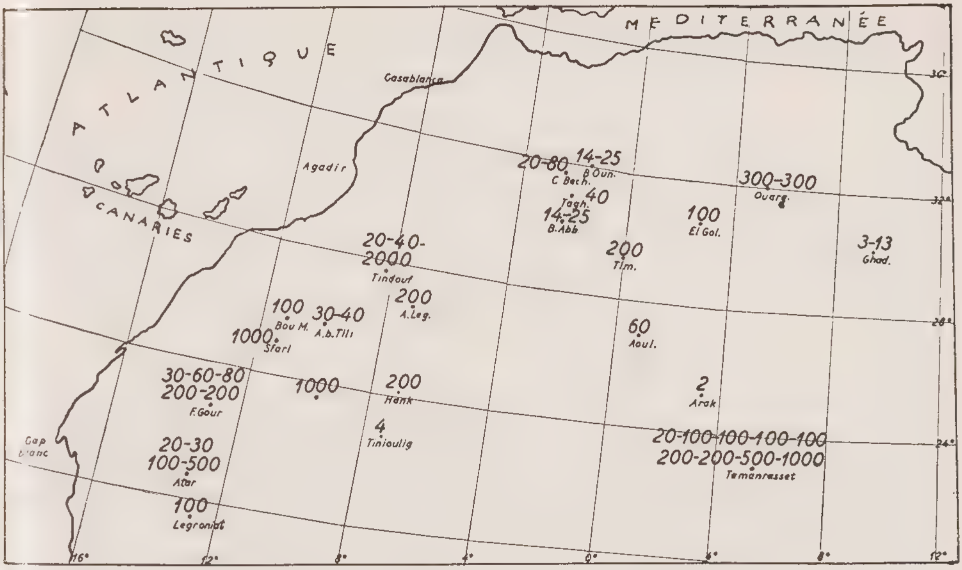


Fig. 5. Les quantités de Cigognes observées dans les différentes localités.

l'observateur dit "un vol important, vraisemblablement plusieurs milliers"). On a aussi plus au nord des renseignements qui montrent de grands nombres de Cigognes, jusqu'à trois cents. De temps en temps il y a aussi de la région occidentale des observations d'un grand nombre de Cigognes (près de Tindouf même plusieurs milliers). Dans d'autres localités furent observés environ mille Cigognes et un nombre de 100 jusqu'à 500 n'est pas exceptionnel non plus.

La carte montre que c'est en assez grand nombre que les Cigognes survolent la région à l'ouest de Tamanrasset et à mon avis ce sont pour la plus part les oiseaux en migration à leur place de nidification au Maroc.

Les materiaux présentés étant basés sur les observations de différentes personnes — pas toujours "très ornithologistes" — il faut naturellement qu'on regarde les résultats avec une certaine dose de prudence. Il semble cependant bien documenté que les Cigognes nordafricaines à leur passage au nord suivent deux routes différentes. Ainsi les Cigognes, qui nichent en Algérie, traversent le Sahara en plus droite ligne, tandis que les Cigognes nichant au Maroc suivent sans doute une route plus occidentale. Mais la fixation de ces routes ne sera pas possible avant que les résultats du marquage des Cigognes de l'Afrique du Nord soient obtenus.

*Discussion*:

(La discussion des exposés de Jespersen et Bouet eut lieu en même temps, puisque leurs thèmes correspondaient.)

E. Schüz: 1) Ich wünsche klargestellt zu sehen, dass Jespersens Kartenreihe I sich nur auf Durchzugs-Storche bezieht. Bekanntlich kommen in N. W.-Afrika die Storche schon wieder etwa von Neujahr ab auf die Nester (Jespersen ergänzt: in Marocko, nicht aber in Algerien). Die heute gezeigte Darstellung schreibt also dem Weisstorch in N. W.-Afrika einen ,,Schleifenzug" zu, was ein höchst bemerkenswerter neuer Gesichtspunkt ist.

2) Gewiss sind *alle* Angaben über Winkel-Flugordnung bei Ciconia ein Irrtum: Verwechslung mit Gans!

3) Gegenüber den Verfassern, besonders Herrn Bouet, möchte ich hervorheben, dass der Zug in dem so schwach gegliederten N. W.-Afrika gewiss nicht so sehr in Form schmaler Strassen erfolgt, wie manchmal behauptet, sondern mehr in weiter Ausbreitung, gewisse Verdichtungen seien aber keineswegs bestritten!

4) Grössere Storchvorkommen an Tschadsee während der Trockenzeit sind glaubhaft von A. Schultze (übersetzt von P. A. Benton, The Sultanate of Bornu, London 1913) mitgeteilt. Darüber und über anderes z. T. unbekanntes Material siehe den soeben erschienenen Bericht: Schüz und Böhringer, Vom Zug des Weiss-Storchs in Afrika und Asien nach den Ringfunden bis 1949, Die Vogelwarte 15/1950, 3, 160—187.

R. Verheyen: Je tiens á l'attention de l'assemblée qu'il paraîtra dans quelques semaines dans le périodique belge d'Ornithologie »Le Gerfaut« fasc. 1+2, 1950, un article dans lequel je traite de la migration de la Cigogne blanche en Afrique et où j'ai développé certaines observations et considérations que j'ai entendues également développé par les Conférenciers MM. Jespersen, Bouet et par M. Schüz, Président de l'assemblée.

## Références

Bouet, G., 1938. Nouvelles Recherches sur les Cigognes Blanches de l'Afrique du Nord. L'Oiseau Rev. Fr. d'Orn.

—— 1950. La Vie des Cigognes. Braun & Cie. Paris.

# Observations on the Migration of the Eastern White Stork (Ciconia ciconia boyciana Swinhoe)

*Axel M. Hemmingsen*

*Copenhagen*

The eastern subspecies of the White Stork *Ciconia ciconia boyciana* Swinh. differs from the European White Stork *C. c. ciconia* (L.) and the Asiatic White Stork *C. c. asiatica* Sew. by its blackish bill and by the greyish tinge on the black area of the wing. It is also a somewhat larger bird. Its breeding range extends from South Yakutia and the Bay of Okhotsk (13), perhaps even from somewhat further north, to Manchuria (9), Korea (1) and Japan (5). It is a resident in Korea and Japan; it does not breed in China proper. A few also winter at the mouth of the Ussuri river, where they eat dead fish thrown upon the ice by the water. I have been unable to trace the sources of statements as to occurrences in winter in Jehol and Chihli (14), and believe such occurrences must be very rare. It is known in winter from Burma, Manipur, Assam and Bengal (2), and in China in 1873 and 1878 abundantly about the Yangtse (3), recently e.g. at Nanking; also down to Fukien (8).

There are very few published reports of observations made during its migration. Authorities on the birds of North China (4, 7, 8, 10, 11, 12, 16, 17, 18) have but a few records each, generally of single birds or minor flocks, and they consider the White Stork very rare.

I had the opportunity of observing this stork on migration for 4 autumns 1942–1945 at Peitaiho Beach, where I saw it resting in the most deserted areas of the plain near dunes, occasionally on sand flats as well, and single specimens feeding in the river. They might scatter over a considerable area but generally were close together; especially, it seemed, as a prelude to leaving. Some of them might fly up now and then. Sometimes flocks passed without settling at all. A large flock of several hundreds might soar for a considerable time in a huge circular vertical band 10–20 birds high, the birds being separated by a considerable distance.

I have brought home and presented to the Copenhagen Zoological Mu-

**My own observations of *C. ciconia boyciana* at Peitaiho Beach.**

Example of date: 6/3 = 6. March. The number of birds seen are given in brackets after each date. The six on 6/3 were seen between Tientsin and Peitaiho.

| Year | Spring | Autumn |
|---|---|---|
| 1942 | | 30/10 (?), 12–13/11 (1000–1500) |
| 1943 | 6/3 (6), 12/3 (19) | 11/11 (17+110), 12/11 (150), 13/11 (200–400), 14/11 (210) |
| 1944 | | 22/10 (40), 4/11 (18+61), 5/11 (200), 6/11 (781 or more+40+200+123), 10/11 (1), 16/11 (2) |
| 1945 | | 6/11 (?), 12/11 (1000–4000), 28/11 (1?) |

seum a specimen shot out of a flock of several hundreds by a hunter as late as 19/11 (in 1944) 35 km south east of Tientsin. Other single specimens of the Eastern White Stork have been shot in North Eastern China in spring, as late as 15/4 (in 1924) just south of Peking (17, p. 210), and in autumn as late as 22/11 (in 1933) 130 km south west of Tientsin (11, Additions, p. 31); whether out of flocks or not is not stated.

Thus, the extreme dates of reliable observations in North Eastern China are 6/3–15/4 and 22/10–22/11.

A couple of times I saw flocks standing in company with the white crane *Grus japonensis* (Müll.). The gregarious instincts of these two bird species were evidently mutually aroused by their similar size and colours when standing, but showed clear-cut differences when they were flushed. For though they all left together toward WSW the white cranes immediately started calling and arranged themselves in line or V-formation, whereas the silent storks, all the time keeping together in a flock, placed themselves in no alinement or order at all. It seems that neither the European nor the Eastern White Stork ever flies in lines or V-formations but always in loose flocks like bustards.

Though it is well known that the flocks of the European White Stork on migration may number thousands or tens of thousands—at the Nile, even hundreds of thousands (6), to my knowledge the migration of White Storks in huge flocks has not been reported before from East Asia. Taczanowski (15) even went as far to state that they "ne se réunissent jamais en grandes troupes."

The passage at Peitaho in the beginning of November when the average temperature is only about 5° C, appears to be very late in comparison with the early departure of the White Stork from Northern Europe in August. The

Eastern White Stork has been observed by Dr. Alfred Hoffmann during a very cold winter (1944–45) at Nanking (verbal communication). And in Japan, where it is a resident, it is seen when snow covers the ground. It seems to avoid cold less than the European form.

More details will appear in "Observations on Birds in North Eastern China. II. Special Part. Spolia Zoologica Musei Hauniensis XI" published by the Zoological Museum of Copenhagen University.

## References

1. Austin, O. L., 1948. The birds of Korea. Bull. Mus. Comp. Zool. Harvard, 101, 1-301 with 1 plate.
2. Baker, E. C. Stuart, 1922-1930. The Fauna of British India. Birds. London.
3. Courtois, R. P. F., 1912. Les oiseaux du musée de Zikawei. Mémoires concernant l'histoire naturelle de l'Empire Chinois, Tome 5, $3^{me}$ Cah., p. 1–98.
4. David, A. and Oustalet, M. E., 1877. Les oiseaux de la Chine. Paris.
5. Jahn, H., 1942. Zur Oekologie und Biologie der Vögel Japans. J. Orn., 90, 1–302, with 5 plates.
6. König, A., 1928. Die Watvögel (Grallatores) Aegyptens. J. Orn., 76. Sonderheft.
7. La Touche, J. D. D., 1920–1921. Notes on the Birds of North Chihli in North China. Ibis. London. 11th Series, 2, 629–671 and 880–920; and 3, 3–48.
8. —— 1925–1934. A Handbook of the Birds of Eastern China, Vol. I–II, London.
9. Meise, W., 1934. Die Vogelwelt der Mandschurei. Abh. Ber. Zool. Mus. Dresden, 18, No. 2, 1–86.
10. Möllendorff, O. F. von, 1877. The Vertebrata of the Province of Chihli with Notes on the Chinese Zoological Nomenclature. J. N. China Asiat. Soc. (n. s.), 11, 41–111 (birds pp. 76–102).
11. Seys, G. and Licent, E., 1932–1934. La Collection d'oiseaux du Musée Hoang ho Pai ho de Tien Tsin. With loose green sheet with Liste d'Errata. Avril 1932. Additions, faites de 1928 à 1933 à la Collection, etc., Avril 1934. Editeurs: Mission de Sien Hsien, Race Course Road, Tientsin 1933. Publications du Musée Hoang ho Pai ho de Tientsin, No. 19 and 31.
12. Shaw, T. H., 1936. The Birds of Hopei Province, Vol. I–II. Fan Memorial Institute of Biology, Peiping (Peking). Zoologia Sinica, Ser. B, 15, Fascicle 1.
13. Stegmann, B., 1930–1931. Die Vögel des dauro-mandschurischen Übergangsgebietes. J. Orn., 78, 389–471 with a map and a plate, 79, 137–236.
14. Steinbacher, F., 1932-1938. Co-author with Hartert of supplement to Hartert: Die Vögel der paläarktischen Fauna. Ergänzungsband. Berlin.
15. Taczanowski, Wl., 1893. Faune Ornithologique de la Sibérie Orientale. Mém. Ac. Sci. St. Pétersb., Sér. VII, 39, parts 1–2.
16. Wilder, G. D., 1940. Migration Notes. The China Journal, 32, 199–204.
17. Wilder, G. D. and Hubbard, H. W., 1924 and 1926. List of the Birds of Chihli Province. J. N. China Asiat. Soc., 55, 156–239, with corrections and additions in 57, 184-194.
18. ——, ——, 1938. Birds of North Eastern China, published by the Peking Natural History Bulletin, Peking, April 1938 (Handbook No. 6). Sales agents: The French bookstore, Grand Hotel de Pékin, Peking, China.

## Round Table Conference on Bird Ringing

The Swedish Executive Committee had decided to arrange a Round Table Conference on Bird Ringing in connection with the papers on Migration. A proposed outline for a discussion programme was drawn up in advance for the purpose of making the discussions as profitable as possible. In order to obtain suggestions for this outline, letters were sent to a number of persons interested in bird ringing in different countries with a request for information regarding their viewpoints and wishes in the question. A great number of suggestions were received. On the basis of these suggestions a preliminary discussion programme was drawn up by Herr Gustaf Danielsson, Stockholm.

The Conference took place on June 16th and was attended by about 50 Members of the Congress.

*Chairmen*: F. C. Lincoln (U. S. A.), Dr. A. Landsborough Thomson (Great Britain).

*Secretaries*: Mrs. E. Lack (Great Britain), Dr. A. Schifferli (Switzerland).

The following resolutions were agreed:—

### *Ring-Marking*

1. It is undesirable at present to attempt to standardise ring-types internationally, but exchange of specimen rings and of information on suitable metals should be arranged between different countries.
2. It is not necessary to standardise the instructions issued to ringers, but specimens of the forms and instructions sent to the ringers should be exchanged between countries.
3. It is undesirable to insist that old birds be marked on the left leg and juvenile birds on the right leg.

4. The ring on a retrapped bird should not be renewed except when it has become very worn.
5. The original record of the data on birds ringed (i. e. the first copy on the official form) should be the one that is sent in to the headquarters of the ringing scheme, and these original records as made by the ringer should be retained there for use, in order to minimise copying errors.
6. It is desirable, as far as possible, that each country should have a single ringing scheme and a single address for use on rings.

### *Publication*

7. It is not practicable to publish full annual lists of recoveries, but selected lists are valuable to stimulate interest in ringing. These selected lists are not suitable as data for detailed analysis of results.
8. Reports on birds ringed or recovered should be published in ornithological journals rather than in separate publications, and it is desirable that those of each ringing scheme should be numbered serially. It is also desirable that publications from ringing centres and ringing reports in journals should be available in the form of separates for serious workers.
9. It is desirable to record the full circumstances of recovery so far as known. The geographical coordinates (put next after the place-name) or other exact indication of the locality should be given, at least where there might be subsequent difficulty in identification; and if the place of recovery cannot be certainly located this should be stated. The original report of the recovery, or covering letter, should be filed. The date of finding of the ring should be recorded when possible, and also whether the ring was returned.
10. The age of birds ringed should preferably be indicated by "nestling" for young still in the nest, and by "pull." or "chick" for nidifugous young not yet full grown. (There was strong divergence of opinion about the term "juvenile," some wishing to retain it and others saying that its meaning was too vague; there is a difference in existing usage between Europe and U. S. A.)
11. Rewards should not be offered for recoveries, except in special circumstances. (The suggestion that publication of the finder's name in sporting papers might advertise the ringing scheme was made by the Spanish delegate, and the value of publicity as a means of stimulating reports of recoveries was stressed by other speakers.)

### *International Organisation*

12. An international coordinating committee should be formed, consisting of the director of each ringing scheme, and with Dr. A. Landsborough Thomson as Chairman and Dr. A. Schifferli as Secretary.
13. Each ringing centre should prepare specimen series of its rings, instructions, forms and records, and send them to all the other centres.
14. Individual ringers wishing to bring up points for discussion should write to their own centres, and only the directors of schemes should correspond with the secretary of the international committee.
15. When a recovery is made abroad, the ringing centre to which it is reported should inform the centre in the country where the bird was recovered.
16. The question of planned ringing and other possibilities of international cooperation should be further considered.

## Bird-Ringing Schemes

known to be operating at present.

*Compiled by W. Rydzewski, London.*

This list includes only those schemes, using rings of their own, which are known to be in actual operation at the time of writing. The schemes are arranged by countries, beginning with European countries in alphabetical order and continuing with countries in other continents.

The information given for each scheme is:—

Title of sponsoring institution or organisation.
Inscription on rings (or on wing-marks, where so stated).
Postal address (in which "as above" indicates repetition of title).

It may be added that in some cases use of the rings is not confined to the country in which the scheme has its headquarters; for example, U.S.A. rings are used also in Canada, and Danish rings in Greenland.

**Belgium**

Institut Royal des Sciences Naturelles de Belgique. "Musée Hist. Nat. Bruxelles". Dr. R. Verheyen, as above, Rue Vautier, 31 Bruxelles, Belgium.

**Czechoslovakia**

Československa ornitologicka společnost. "N. Museum Praha ČSR". Ing O. Kadlec, Narodni Museum, Praha II, Czechoslovakia.

**Denmark**

Dansk ornitologisk Central. "P. Skovgaard Viborg Danmark" P. Skovgaard, Viborg, Denmark.

Zoologisk Museum. "Zoological Museum Copenhagen". Dr. H. Johansen, as above, Krystalgade, Copenhagen, Denmark.

**Finland**

Yliopiston Elaintieteellinen Museo. "Mus. Zool. Helsinki Finland". Dr. O. Kalela, as above, P. Rautatienkatu 13, Helsingfors, Finland.

Suomen Riistanhoito-Säätiö, Riistantutki muslaitos. "Riistasäätiö Helsinki" (wing-marks). J. Koskimies, as above, P. Rautatienkatu 13, Helsingfors, Finland.

**France**

Station Ornithologique de Versailles. "I. R. A. Versailles France". J. Giban, Centre national de Recherches agronomiques, Route de St. Cyr, Versailles, France.

Station Ornithologique, Muséum National d'Histoire Naturelle. "Oiseaux Museum Paris". Prof. E. Bourdelle, as above, Rue de Buffon, Paris, France.

**Germany**

Institut für Vogelforschung Vogelwarte "Helgoland". "Vogelwarte Helgoland Germania". Prof. Dr. R. Drost, as above, Vogelwarteninsel, (23) Wilhelmshaven, Germany.

Vogelwarte Radolfzell. Institut für Vogelforschung der Max Planck Gesellschaft zur Förderung der Wissenschaften. "Vogelwarte Radolfzell Germania". Dr. R. Kuhk, as above, (17b) Schloss Möggingen üb. Radolfzell (Bodensee), Germany.

**Great Britain**

Bird-Ringing Committee of the British Trust for Ornithology. "British Museum Nat. Hist. London". Miss E. P. Leach, c/o Bird Room, British Museum (Natural History), Cromwell Road, London, S.W. 7, England.

**Holland**

Rijksmuseum van Natuurlijke Historie. "Mus. Nat. Hist. Leiden Holland". J. Taapken, as above, Leiden, Holland.

**Hungary**

Magyar Madartani Intezet. "M. Ornith. Központ Budapest". Dr. A. Keve, Magyar Madartani Intezet, Mezögazdasagi Muzeum, Budapest-Varosliget, Hungary.

**Iceland**

Fuglamerkingar Natturugripasafnid. "Mus. Nat. Reykjavik Iceland". Dr. F. Gudmundsson, as above, P. O. Box 532, Reykjavik, Iceland.

**Italy**

Osservatorio Ornitologico Ligure. "Bologna Univ. Ge. Italy". Dr. R. Macaggi, as above, Via Anton Maria Maragliano 8 cancello, Genova, Italy.

Osservatorio Ornitologico di Ancona. "Bologna Univ. Italia Ana." V. Ortali, as above, Via Rossini 13, Ancona, Italy.

Osservatorio Ornitologico Toscano. "Univ. Bologna Osserv. Pisa Italia". Prof. dr. F. Caterini, as above, Via Bonanno 12, Pisa, Italy.

Osservatorio Ornitologico della Mesola. "Zoologia Bologna Italia". Dr. L. Leporati, as above, Mesola (Ferrara), Italy.

**Norway**

Statens Viltundersökelser. "Zool. Museum Oslo". Dr. O. Olstad, Zoologisk Museum, Oslo, Norway.

Stavanger Museum. "Stavanger Museum Norway". H. Holgersen, as above, Stavanger, Norway.

Universitetets Zoologiske Laboratorium. "University Oslo". Prof. dr. H. Broch, as above, Oslo-Blindern, Norway.

**Poland**

Stacja Ornitologiczna, Panstwowe Muzeum Zoologiczne. "Mus. Zool. Polonia Varsovia". J. B. Szczepski, as above, Wilcza 64, Warszawa, Poland.

**Russia**

Centralnoye Byuro Kolcevanya. "Moskwa". V. Makarov, as above, Neglinnaya 21, Moscow. U.S.S.R.

**Spain**

Grupo de Ciencias Naturales Aranzadi. "Aranzadi-Museo San Sebastian Espana". As above, Museo de San Telmo, Plaza de Ignacio Zuolaga, San Sebastian, Spain.

**Sweden**

Ornitologiska Stationen i Göteborg. "Museum Göteborg Sweden". V. Fontaine, Göteborgs Naturhistoriska Museum, Göteborg 11, Sweden.

Naturhistoriska Riksmuseets Vertebratavdelning. "Riksmuseum Stockholm". Miss G. Vestergren, as above, Stockholm 50, Sweden.

Svenska Jägareförbundet. "Sv. Jägareförbundet Sweden" (wing-marks). N. Höglund, Bergvik 1, Sweden.

**Switzerland**

Vogelwarte Sempach. "Vogelwarte Sempach Helvetia". Dr. A. Schifferli, as above, Sempach, Kanton Luzern, Switzerland.

**Yugoslavia**

Ornitoloski Zavod u Zagrebu. "Ornit. Institut Zagreb Jugoslav.". Prof. R. Kroneisl, as above, Zagreb, Ilirski trg 9, Yugoslavia.

**Canada**

Jack Miner Migratory Bird Foundation. "Write Jack Miner Kingsville Ontario Canada". M. F. Miner, as above, Kingsville, Ontario, Canada.

**United States of America**

Fish and Wildlife Service. U. S. Dept. of the Interior. "Notify Fish & Wildlife Service Washington D. C." Seth H. Low, Patuxent Research Refuge, Laurel, Maryland, U.S.A.

**Egypt**

Zoological Gardens at Giza. "Zoo Cairo". Zoological Gardens, Giza, Cairo, Egypt.

**South Africa**

South African Ornithological Society. "Pretoria Zoo". Dr. E. H. Ashton, P. O. Box 591, Bulawayo, Southern Rhodesia, Africa.

The Government Guano Islands Administration. "UG". The Superintendent, Union Govt. Guano Islands Office, 32 Riebeck St., Cape Town, South Africa.

**India**

Bombay Natural History Society. "Inform Nat. Hist. Society Bombay". Salim Ali, as above, 114 Apollo St., Bombay, India.

**Japan**

Forestry Agency, Ministry of Agriculture and Forestry. (Three Japanese characters). Game Management Section, Ministry of Agriculture and Forestry, Tokyo, Japan.

**Australia**

Commonwealth Scientific and Industrial Research Organization. "Notify Fauna Board Hobart Tas. Australia". As above, 314 Albert St., East Melbourne C. 2, Australia.

**New Zealand**

Department of Internal Affairs. "Return Wildlife Serv. Govt. Bldgs. Wtgn. N. Z." As above, P. O. Box 7, Government Buildings, Wellington C. 1, New Zealand.

Ornithological Society of New Zealand. "Send Dominion Museum New Zealand." T. M. Cunningham, 39 Renall St., Masterton, New Zealand.

# Recent Advances in the Study of Bird Behaviour

*N. Tinbergen*

*Dept. of Zoology and Comparative Anatomy,*
*University of Oxford*

## Introduction

Since the last congress, a remarkable development has taken place in the field of bird ethology, as in animal ethology in general. We could characterise the last two decades, and above all the last twelve years, as a period of establishing and consolidating the "biological study of behaviour." By this I mean that it is now becoming generally recognised that behaviour is a life process which can be observed and recorded objectively just as any other life process, and that it is open to biological study in its widest sense. This means that, as in other fields of biology, we have to do with functioning structures—involving, in behaviour, mainly sense organs, nervous system, and muscle system—the observation of which reveals three great problems. These problems are fundamentally the same all through biology. Their study gives rise to what Huxley has called the "three main categories of biological fact" (Huxley, 1940). These problems are:

1) The problem of causation. We want to know the underlying causal relationships responsible for behaviour.
2) The problem of biological significance. We must gain an insight into the way the observed processes contribute toward the maintenance of the highly improbable, unstable state of matter we call an organism.
3) The historical problem, or the problem of evolution.

The rapid emancipation of bird ethology has been made possible by the participation of ornithologists of many different types. To the student of animal behaviour (who cannot help studying human conduct—including his own—as well as animal behaviour) it is highly interesting to see how different is the approach of the various workers in this field. Some are fascinated by "a bird" or by "birds," others by "the Bird" in an abstract sense, others again by a problem, which they study in a variety of birds. Some prefer to watch wild birds in the field, others raise them by hand and keep them as pets. Some are inclined to describe, others prefer experimentation, others again theorise on observational data, thus pointing the way to possible explanations without feeling inclined to provide proof by experiment. It is a lucky circumstance that our science attracts all these different types of ornithologists; together they guarantee a broad and many-sided approach. Yet among all these workers there is one who has done more than any one else for the promotion of ethology as a genuine biological science; I feel it my duty to pay tribute to the work of Konrad Lorenz in this review of a period dominated by his work. His pioneer work in outlining the scope and aims of the biological study of behaviour, in clarifying the problems and placing them in the framework of general biology, has been extremely fertile, and marks the beginning of a period of rapid development.

The clear biological formulation of the problems has led to a recognition of the fundamental relationship of ethology with other fields of biology, and this has widened the interests of behaviour students considerably. As a matter of fact, it has widened it to such an extent that it is impossible to outline ethology and to mark the boundaries separating it from other fields, such as neurophysiology, ecology, evolution study. This widening of the field renders it impossible for me to review it satisfactorily in 45 minutes' time. My speech therefore will be limited in several respects. (1) I will give relatively little attention to work on low planes of integration, where ethology borders upon physiology. However tempting it might be to dwell upon recent work on sensory reception, or on the splendid work of von Holst (1943) on the mechanics of bird flight, I cannot do so. (2) Also, ecological aspects of behaviour, such as territory, habitat selection, prey-predator relationships, cannot be discussed. (3) Lastly, the evolution problems can only be touched.

Even with these restrictions, a choice had to be made. Naturally, this choice has been subjective.

I will arrange my address on the basis of the three major problems mentioned. It is due to the participation of such diverse types of workers that progress in our field is only to a minor extent dependent on papers especially devoted to one problem. The literature on bird behaviour contains many papers of a monographic character, which are at the same time descriptive and explanatory. Mrs Nice's Song Sparrow paper (1943), Makkink's Avocet (1936), Kortlandt's Cormorant papers (1940 a, b), Laven's monograph on the Ringed Plover (1940), etc., are attempts at descriptive monographs, or ethograms. However, each of them contain manifold attempts at explanations of special phenomena. It is typical that the explanatory parts are more fragmentary than the descriptive parts: here a discussion on special stimuli releasing certain responses, there a discussion of the function of territory, there again hypotheses on the origin of courtship movements, and so on. In spite of the fragmentary nature of each paper, together, and together with numerous short papers, they begin to give a broad picture of bird behaviour, of its immense diversity in detail, and, at the same time, of the remarkable uniformity of underlying principles.

I should mention here two recent books on bird behaviour which have had a great influence. Lack's "The Life of the Robin" (1943) is outstanding as an example of the valuable contribution that modern behaviour study can make towards a better understanding of one of our commonest birds; also, it is admirably suited as a general introduction to bird ethology. Armstrong's "Bird Display" (1942), which appeared in second impression under the wider title "Bird Display and Behaviour" (1947), has the merit of calling attention to an immense number of publications which are scattered over a wide variety of journals and books.

Of course the recent advances in ethology are not due to work on birds alone, but also to studies on other groups, notably fish. Birds however are in many respects excellent objects and that is why a sketch of bird ethology may give a fair idea of the state of ethology in general. As a matter of fact, ornithology has played a leading part in the development of modern ethology.

## Causation

Perhaps the most general conclusion taking shape at present is the following: all behaviour, however variable and plastic it may be, is based on a limited set of mechanisms, in which sense organs, nervous system, and muscles take part. These mechanisms are the foundations of what are usually called instincts. The variability of behaviour, although admittedly very great, is nevertheless limited. It is due to complexity. This complexity is based upon a hierarchical organisation, in which relatively rigid elements are integrated into systems. Simple muscle contractions are coordinated into relatively simple systems (for instance antagonistic pairs), these systems are coordinated with other, similar systems into systems of a higher order (for instance left and right leg); these again are coordinated with other equivalent systems, and so on. On each level in this highly complex hierarchy there is a dependence on special causal factors. There are, for instance, sensory stimuli which release fighting ("intruder in territory"). There are also factors, such as sex hormones, which do not confine their influence to reproductive fighting, but which activate the whole reproductive instinct, of which reproductive fighting is merely a part. At each level a number of causal factors are at work, each variable and giving rise to an enormous variety of effects. Moreover, the causal factors influence each other.

This picture of instincts as mechanisms is based on facts of many kinds, of which only a few will be reviewed. Perhaps the strongest support in favour of it is the fact that really intensive acquaintance with a species by years of study enables the observer, with growing reliability, to predict behaviour on the basis of knowledge of internal and external conditions.

### *External stimuli*

Research on the influence of external stimuli covers two problems. (1) The first step is to find out which processes in the external world the sense organs can receive. (2) The next step is to find out which stimuli are actually causing behaviour of a given type. Failure to distinguish between these two problems may be a serious obstacle in ethological research.

The *capacities of the sense organs* of birds have been summarised by Pumphrey to whose valuable paper I can refer (Pumphrey 1948). I may comment on two points. Colour discrimination is now established in more species than mentioned in Pumphrey's paper, viz., in the Song Thrush (*Turdus e. ericetorum* Turton, Van Eck, 1939) and in the Little Owl (*Athene noctua vidalii* A. E. Brehm, J. Meyknecht, 1941). In the Song Thrush it was found that the ability to distinguish between colours was lost at low intensities of illumination, when intensity discrimination was still possible; the change coincided with a change in shape and position of rods and cones. The Little Owl is equally capable of colour discrimination. The sensitivity for red is low, but red can be distinguished as a colour. In neither species can visually guided behaviour be released by either ultraviolet or infra-red light. Van der Plank's claim (1934) that owls can see infra-red waves therefore does not hold for the Little Owl, nor does it hold for *Otus asio naevius* (Gmelin) (Hecht & Pirenne, 1940).

There is still a serious gap in our knowledge of sensory capacities: in spite of intensive research it is still uncertain whether homing or migrating birds use an unknown type of sensory reception or not. Neither Ising's theory (Ising 1945) nor Yeagley's work (1947) have met with approval (see Thorpe, Wilkinson & Wojtusiak, 1949). Griffin showed, in a valuable paper (1944) that there are many possible explanations on the basis of the achievements of the known sense organs and their cooperation. In my opinion, the most promising work is that reported by G. Kramer, who was the first to discover directed "flight" in caged migrants and who succeeded in influencing the direction experimentally. (See Kramer, 1951).

The behaviour student has special aims in studying the sense organs' capacities, aims differing from those of the student of sense physiology. I can do no more than just mention the four main problems.

a) Sensitivity. It is necessary to know the range and limits of sensory receptivity, in both a quantitative and qualitative respect. Applied to light receptors, we must know which part of the spectrum can be seen. Further, we have to know the highest and especially the lowest limit of intensity that can be seen. Applied to the ear, these problems are that of the range of frequencies and that of the range of intensities.

b) The next problem is that of discrimination. This, again, has a qualitative and a quantitative aspect. How many colours can be distinguished, and how many shades? Applied to the ear, the qualitative problem concerns pitch discrimination, and the quantitative problem is that of intensity discrimination.

c) Another problem is that of power of localisation in space. For the eye, this means visual acuity (in which birds may well be at the top of the animal kingdom); for the ear it means spotting the direction from which a sound comes.

d) The most difficult problem, and yet the most important for the behaviour student, is that of discrimination of patterns. This is especially interesting in the eye, where patterning in space (form) and in time (movement) are of extreme importance. In the case of the ear, patterning in time enables an animal to recognise melodies.

In all these fields, much research is still needed. We know from field observations that recognition of form, movement, and melodies may be better in birds than in ourselves.

*Actual stimuli.* Many observations and several experimental investigations have substantiated Lorenz's thesis (1935, 1937) that instinctive behaviour is released by relatively few stimuli of a rather generalised type. The negative side of this conclusion is of special interest: many properties of an outside object or situation which could be percieved by the animal may be entirely or largely ineffective in releasing a given reaction. The effective stimuli, called sign stimuli (*Schlüsselreize*), are different for each reaction. As an instance I may mention the results obtained with the begging response of the Herring Gull chick (Tinbergen & Perdeck, 1950); for a review of similar facts see Tinbergen (1951).

### *Spontaneity*

It is obvious that behaviour is very rarely, if ever, purely reactive. There are always internal factors at work which determine the readiness to react to external stimuli, and which even drive the bird to explosive behaviour. All these factors seem to be specific, that is they influence special instincts.

Some of these internal factors are hormones. Research in this field is still in its beginning. Whereas we know from various studies that some sexual activities can be stimulated by sex hormone injections in young, in females or in castrated individuals (song in Canaries, Shoemaker, 1939; crowing, "waltzing" and "tidbitting" in domestic Cocks, Davis & Domm, 1943; Zitrin, 1942, etc.; for a review see Beach, 1948); we still have only the vaguest ideas about the influence of sex hormones on the reproductive pattern as a whole. For an insight into the nature of the influence of hormones on behaviour it is first of all necessary to study the total influence; we must find out whether the hormone activates minor elements or major patterns. Evidence thus far available seems to indicate that hormones act on the major patterns, and since major patterns are characterised by the type of coordination and not by the individual muscles involved, this points to an influence on relatively high centers, presumably those at the top of major instincts. We cannot exclude the possibility of peripheral influence as well, but this alone could never account for the appearance of ordered behaviour patterns. The responsibility for order is with the central nervous system.

Apart from hormones, internal sensory stimuli may cause spontaneous behaviour. This applies for instance to feeding behaviour, in which stimuli derived from the stomach wall play a part, at least in mammals.

There has been uncertainty, and much discussion, about the question whether the central nervous system is able to produce spontaneous discharges in instinctive centers without any hormonal or sensory stimulation, whether internal or external. The evidence regarding "automatic" activity (Adrian & Buytendijk, 1931; von Holst, 1937; Gray, 1939; Lissmann, 1946; Weiss, 1941) is still contradictory. As I have tried to show elsewhere (Tinbergen, 1951) the terms "automatic" and "intrinsic" have been applied to two different phenomena, the initiation of movements, and the coordination or patterning. The uncertainty concerns the initiation rather than the patterning, which is partly intrinsic as shown by the work of Lissmann, Gray, von Holst, Weiss and others. As regards the initiation, most of the evidence seems to indicate that total absence of external stimulation, such as realised in an animal with a totally deafferentated spinal cord, abolishes movement. A certain inflow of diffuse sensory impulses, such as seems to be provided by at least some sense organs even when screened from external stimulation (von Holst, 1950) appears to be necessary for locomotion (Lissmann, 1946).

In the discussions on this problem, as recently held in Cambridge (S. E. B. Symposium, 1950) undue emphasis was laid, perhaps, on the relation of spontaneity of behaviour and "automatic" activity of the central nervous system. Even if "automatic" activity of the central nervous system would be shown to be non-existent, the evidence on the influence of hormones, of internal sensory stimuli and of "diffuse" inflow of impulse from the external sense organs is sufficient to show that behaviour is often "spontaneous," that is, independent of sign stimuli. This justifies and even necessitates the use of terms as "drive," "motivation" etc.

A few words must be said about the specificity of all these factors. An animal is rarely, if ever, active in a mere general sense. Its activity has usually, or maybe always, a special quality. It is either hunting, or nesting, or incubating, or preening, or sleeping, etc. Often the intensity of the activation is very low and can only be seen by subtle signs, such as a ruffling of the feathers, wide opening of the eyes, or fixating certain objects, or stretching the neck. One often reads about "general excitement" in cases where the excitement (a psychological expression used to denote the state of activation) is obviously not general but, for instance, reproductive, or, more restricted even, sexual, or aggressive, or broody. One of the main aims of behaviour study is to find out of which type the excitement is, or in objective language, which of the instincts is or are activated.

### *Releasing and directing stimuli*

Lorenz (Lorenz & Tinbergen, 1938) has pointed out that external stimuli may influence behaviour in two different ways. Some stimuli merely release a reaction; the influence of such releasing stimuli may not go beyond this initial release, and the reaction—often a part of a chain— goes on for some time after it has been released. This is possible because so many movements are intrinsically patterned. Other sensory stimuli are responsible for the spatial guidance of movements; they exert their influence throughout the movement and release corrections as soon as the animal deviates from the oriented position. The mechanisms set in motion by these releasing and directing stimuli, respectively, can be compared with the two mechanisms responsible for the course of a steamship. The propeller mechanism is released and may go on for a long time after release; the ship's movements are directed by the rudder mechanism which is continuously being steered and reacts to stimuli quite different than those controlling the propeller mechanism. In animal behaviour an analogous distinction can often be made (Lorenz & Tinbergen, 1938; Tinbergen & Kuenen, 1939); it forces us to distinguish between "fixed patterns" (*Erbkoordinationen*) and spatial correction movements, a distinction which enables us to see the differences between the two types of mechanisms involved more clearly and which will facilitate their analysis. Research in this field is most urgently needed.

### *Appetetive behaviour and consummatory act*

Craig (1918) was the first to point out that behaviour, if complete, leads to the performance of a relatively simple act, which he called the consummatory act, and that the animal seems to strive towards its performance by means of a variable and adaptive type of behaviour, in fact that the animal seems to have an appetite towards the performance of its consummatory acts. Lorenz showed that the activities called by him "instinctive activities" (*Instinkthandlungen*) were such consummatory acts; he called the preparatory behaviour leading to the consummatory act "appetitive behaviour." He argued that it is the performance of the consummatory act which puts an end to the appetitive behaviour. In other words, the consummatory acts above all consume the "drive," or specific motor impulses.

It is worth while that this distinction, made necessary by the recognition that the appetitive behaviour and the consummatory act are quite different types of behaviour, means a splitting-up of the total behaviour chain into two very unequal parts. The consummatory act in its relative simplicity and rigidity is much more easily analysed than the appetitive behaviour, which is rather "the total behaviour minus one simple element, the consummatory act."

In cases of low activation of an instinct, it is the initial phase of the appetitive behaviour that is first performed. These incomplete activities have been recognised long ago and have been named intention movements by Heinroth (1911). Much of the apparent variability in behaviour is due to differences in intensity of the activation, and it is, therefore, of great practical importance to be able to recognise the various, often many, intensities of one and the same type of behaviour. Further, as we shall see, intention movements have in many cases acquired the secondary function of releasers; therefore, they are of great importance to the student of animal sociology.

### *Displacement activities*

The discovery and analysis of displacement activities, by Kortlandt (1940b) and by Tinbergen (1939a, 1940) was another step in the unraveling of behaviour patterns. A displacement activity is an activity caused by a drive other than the instinct to which it belongs. The evidence suggests that it is always the result of a surplus of motor impulses of an activated instinct. Whenever an instinct is strongly activated, but certain circumstances render performance of the appropriate movements impossible, the motor impulses find an outlet through the executive mechanisms of another instinct. Thus in territorial boundary clashes fighting and escape may be activated in each individual at the same time, and, being incompatible, their activation gives rise to "irrelevant" movements such as preening, nest-building, eating. Such irrelevant movements are, in this case, to be interpreted as displacement activities; they are "fed" by other drives than that to which they belong. Or, when an animal, usually a male, is strongly sexually activated but the mate fails to produce the stimuli necessary to release his final copulatory response (the consummatory act), the male may perform an irrelevant act such as preening, nest-building, etc.

Such displacement activities are characteristic of the species, and of the situation. Fighting Starlings preen their plumage, but fighting Herring Gulls males (*Larus a. argentatus* Pont.) perform nest building movements, and fighting Domestic Cocks make feeding movements. This demonstrates the need of caution in the interpretation of the activated instinct: nesting behaviour does not always betray an activated condition of the nesting instinct but may be "fed" by the aggressive instinct.

The study of displacement activities confirms once more the existence of rigid mechanisms underlying behaviour. It further enables us to assess the intensity of a drive even if this drive does not lead to the performance of its own consummatory acts. Finally, displacement activities have often releaser function.

There are many more highly interesting aspects to this phenomenon, such as the light it throws on sleep as a consummatory act, and the usefulness of displacement activities as tools for the study of instinct, etc., but the time does not allow to elaborate these aspects. One example, however, may be discussed of intention movements and displacement activities as constituents of threat display, in which they fulfill the part of releasers with an intimidating function.

The Herring Gull has three threat postures: the upright threat posture, "grass pulling," and "choking."

In the upright threat posture the neck is stretched, the head is pointing downward, and the wings may be slightly lifted: three components of the intention movement of actual attack (trying to come on top of the opponent, pecking, delivering wing blows). When close to the opponent, the bird halts and withdraws the head so that the stretched neck assumes a more vertical position. This is a component of defense, of withdrawal. The stronger the tendency to withdraw, the more the neck is brought back. This threat posture therefore is clearly recognisable as the combined intention movements of the two antagonistic drives: attack and withdrawal, or escape.

When the intensity of both participating drives increases, the mere intention movements are not sufficient as outlets, and then the bird shows displacement nest building. When the mate does not actively join the fight, we see grass pulling. At relatively low intensity, the bird picks up nest material, and throws it down with a sideways, jerking head movement. When more intense, material is selected that offers resistance to attempts to pull it out (roots, large grass tufts) and then the bird pecks at it vigorously and pulls at it for all it is worth. In other words, the bird selects nest material, but treats it as it would treat the opponent in a fight. Some components of the fighting drive are superimposed on the displacement activity.

If, during a fight of high intensity, the mate joins the fighting bird, another displacement activity derived from the nestbuilding pattern is shown: "choking," occasionally accompanied by leg scraping.

This analysis shows the use of a clear recognition of intention movements and displacement activities in recognising the nature of the underlying drives. All aggressive behaviour of the Herring Gull, at first sight a curious mixture of relevant and irrelevant movements, is caused by varying degrees of activation of two drives: attack and escape. Between pure attack and pure flight there are intermediates or mixtures, giving rise to what seem to be entirely "new" movements.

### *Learning processes*

Much in a bird's behaviour pattern is innate. During individual life various changes occur, mostly in the sensitivity to stimuli, but—rarely—also in the form of the motor pattern. Some of these changes are due to growth processes in the instincts, mainly in the central nervous structures involved, others are learning processes. The learning phenomena have been treated admirably by Thorpe (1951) to whose paper I may refer. In my opinion, Thorpe's contribution is outstanding because it is based on evidence of various types of learning as taking place in normal behaviour and not merely of learning in highly impoverished and strained laboratory conditions.

## Biological significance

At present there is, in many fields of biology, rather an overemphasis on problems of causation. In other fields biological significance is often considered, but mainly for the purpose of evolutionary study. I should like to stress the need of study of biological significance not only for the sake of studying selective value, but also for its own sake. Insight into the way in which a life process helps the individual or group in maintaining itself adds an essential quality to our biological picture. The following instance may illustrate this.

In various gulls and in other birds "foot-paddling" is often observed. It is usually done on wet soil or in shallow water. It has been repeatedly observed that Herring Gulls, "foot-paddling" in the meadows bring earthworms to the surface which are then eaten. Several species of gulls also practise it on the sea shore, and it is often suggested that here their paddling brings marine worms to the surface. However, so far I know, no marine worms react to soil disturbances by coming to the surface, as some earthworms do. I believe that we have to do with two entirely different functions of one movement. Foot-paddling on the shore is, according to my observations, usually done in shallow pools, and its function here is probably to whirl up small invertebrates. When done in the grass it serves to bring earthworms to the surface. Analogous behaviour is found in other birds. Lapwings (*Vanellus vanellus* (L)) bring up earthworms by quick trembling motions of one foot (Portielje, 1927); Phalaropes (*Phalaropus lobatus* L.) whirl up motionless prey by "pirouetting" (Tinbergen, 1936). Whatever the solution of this problem, its present state shows well how unsatisfactory is uncertainty about the biological significance of an activity.

The problem of anting in birds is in a still more confused state. As Chisholm (1944) points out, there are a number of hypotheses or rather guesses about its biological significance, none of which are decisively supported by facts.

By way of contrast, our growing insight into the biological significance of colour patterns may be mentioned. Apart from cryptic colours, and various types of conspicuous coloration, all playing a part in the defense against predators, the releaser type of colour marking begins to be understood (Lorenz, 1935; Tinbergen, 1948 a). The keen interest in this problem, which sometimes assumes the shape of vigorous criticism of the whole idea of releasers (Rand, 1941, 1942; Aronson, 1949) shows how deep-rooted the interest in biological significance is.

An important tool in this type of study is comparison, which enables us to see convergencies among non-homologous behaviour patterns, and divergencies among homologous patterns. As an instance of convergence the various ways in which birds fasten material into their nests may be mentioned. Cormorants (*Phalacrocorax carbo sinensis* (Shaw & Nodder), Crows and several other birds make trembling motions with a twig until it gets stuck in the nest (Kortlandt, 1940 a), Long-tailed Tits (*Aegithalos caudatus* (L.)), Icterine Warblers (*Hippolais icterina* (Vieill.)) and Chaffinches (*Fringilla c. coelebs* L.) weave spiders' silk over newly added nest material (Van Dobben, 1949; Maxse, 1951; Tinbergen, 1942 a); Great Reed Warblers [*Acrocephalus a. arundinaceus* (L.)] "paste" the material together by using soaking wet material (Kluyver, 1949). An example of divergence is found in the varying ways in which incubating birds react to predators. A Nightjar (*Caprimulgus europaeus* L.) sits very tightly and does not leave the nest until a predator is very close, whereas a gull (*Larus*) or a tern (*Sterna*) leaves its nest at the slightest alarm. This of course is correlated with cryptic colouration, of the adult in the first case, of the eggs in the second case. As an extreme case of divergence we may consider the absence of certain patterns in some animals. It is quite possible for instance that a closer study of mating behaviour in Amphibians, where reproductive fighting is usually absent, will teach us something about the significance of reproductive fighting in animals such as birds.

## History

No biological picture is complete without a consideration of evolution, the main and ultimate problem of biology.

Very little is known about the way behaviour changes in the course of evolution. We do know that much is genetically determined. This applies not only to the simpler elements of behaviour, but also to relatively complicated patterns such as locomotion (Weiss, 1941) and other fixed patterns (Lorenz). However, how mutation in its widest sense affects behaviour is scarcely known.

Comparison of behaviour patterns and behaviour elements in closely related species and subspecies can be used for the purpose of tracing homologies. This work has been started by Whitman in pigeons (Columbidae, 1919); a recent study of great importance is Lorenz's paper (1941) on surface feeding ducks (Anatinae). Much more work is needed on comparison of species and subspecies, and after this, cross-breeding will be a primary task of the future.

One of the most promising problems in this field is the origin of releasers and their differentiation in closely related groups, as has been repeatedly stressed by Lorenz, whose duck paper contains several pertinent results. For instance, displacement preening is a constituent of courtship of the drakes of many species; the form of the movement is different in different species, and always closely correlated with conspicuously coloured parts of the plumage which are demonstrated by the movement.

A similar study has been made on intention movements by Daanje (1950), who was able to trace several principles of evolutionary change.

Comparison for the purpose of evolution study may be carried out on higher levels also, but here still more extensive studies are required for a reliable descriptive basis. Davis' papers on the nesting behaviour of the Anis (*Crotophaga* and *Guira*) (summary in Davis, 1942) are examples of this type of approach.

## Conclusion

This sketchy review is not primarily a review of results obtained; it rather is a review of possibilities. The discovery of possibilities for research is, to many of us, the most fascinating phase in a science. It seems to me that the present state, characterised by a faith in the possibilities of objective biological study of behaviour, is full of promise for the future. I may conclude by expressing the hope that our science may be fortunate enough to attract in the future, as it has done in the past, "birds of diverse plumage," so as to ensure a broad development.

## References

Adrian, E. D. and F. J. J. Buytendijk, 1931. Potential changes in the isolated brain of the goldfish. Jour. Physiol. 71, 121–135.

Armstrong, E. A., 1947. Bird Display and Behaviour. London.

Aronson, L., 1949. An analysis of reproductive behavior in the mouthbreeding Cichlid fish, *Tilapia macrocephala* (Bleeker), Zoologica. N. Y. 34, 133–158.

Beach, F. A., 1948. Hormones and Behavior. New York.

Chisholm, A. H., 1944. On the problem of "anting." Ibis 86, 389–405.

Craig, W., 1918. Appetites and aversions as constituents of instincts. Biol. Bull. 34, 91–107.

Daanje, A., 1950. On locomotory movements in birds and the intention movements derived from them. Behaviour 3, 48–98.

Davis, D. E., 1942. The phylogeny of social nesting hebits in the Crotophaginae. Quart. Rev. Biol. 17, 115–134.

Davis, D. E. and L. V. Domm, 1943. The influence of hormones on the sexual behavior of domestic fowl. Essays in biology, in honor of Herbert M. Evans, 171–181.

Dobben, W. H. van, 1949. Nest building technique of Icterine Warbler and Chaffinch. Ardea 37, 89–97.

Eck, P. J. van, 1939. Farbensehen und Zapfenfunktion bei der Singdrossel, *Turdus e. ericetorum* Turton. Arch. néerl. Zool. 3, 450–499.

Gray, J., 1939. Aspects of animal locomotion. Proc. Roy. Soc. London B. 128, 28–62.

Griffin, D. J., 1944. The sensory basis of bird navigation. Quart. Rev. Biol. 19, 15–31.

Hecht, S. and M. H. Pirenne, 1940. The sensibility of the nocturnal Long-eared Owl in the spectrum. Jour. Gen. Physiol. 23, 709–717.

Heinroth, O., 1911. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. Verh. V. Internat. Ornithol. Kongr. Berlin, 589–702.

Holst, E. von, 1937. Vom Wesen der Ordnung im Zentralnervensystem. Naturwiss. 25, 625–631, 641–647.

—— 1950. Die Arbeitsweise des Statolithenapparates bei Fische. Zs. vergl. Physiol. 32, 60–120.

—— 1943. Ueber „künstliche Vögel" als Mittel zum Studium des Vogelflugs. Journ. f. Ornithol. 91, 406–447.

Huxley, J. S., 1940. Evolution, the Modern Synthesis. London.

Ising, G., 1945. Die physikalische Möglichkeit eines tierischen Orientierungssinnes auf Basis der Erdrotation. Ark. f. Mat., Astron. och Fysik 32 a, 1–23.

Kluyver, H. N., 1949. De nestbouw en het huwelijksleven van de grote karekiet. In: In het voetspoor van Thijsse, Wageningen, 23–36.

Kortlandt, A., 1940 a. Eine Übersicht der angeborenen Verhaltensweisen des Mittel-europäischen Kormorans (*Phalacrocorax carbo sinensis* (Shaw & Nodder)), ihre Funktion, ontogenetische Entwicklung und phylogenetische Herkunft. Arch. néerl. Zool. 4, 401–442.

—— 1940 b. Wechselwirkung zwischen Instinkten. Arch. néerl. Zool. 4, 442–520.

Kramer, G., 1951. Eine neue Methode zur Erforschung der Zugorientierung und die ersten Ergebnisse. Proc. X. Internat. Ornithol. Congress, Uppsala (in press).

Lack, D., 1943. The Life of the Robin. London.

Laven, H., 1940. Beiträge zur Biologie des Sandregenpfeifers (*Charadrius hiaticula* L.). Journ. f. Ornithol. 88, 183–288.

Lissmann, H. W., 1946. The neurological basis of the locomotory rhythm in the spinal dogfish (*Scyllium canicula, Acanthias vulgaris*). II. The effect of deafferentation. J. Exp. Biol. 23, 162–176.

Lorenz, K., 1935. Der Kumpan in der Umwelt des Vogels. Journ. f. Ornithol. 83, 137–213 and 289–413.

—— 1937. Ueber die Bildung des Instinktbegriffs. Naturwiss. 25, 289–300, 307–318, 324–331.

—— 1939. Vergleichende Verhaltensforschung. Zool. Anz. Suppl. Band 12, 69–102.

—— 1941. Vergleichende Bewegungsstudien an Anatinen. Journ. f. Ornithol. 89. Festschrift Heinroth 194–294.

—— 1943. Die angeborenen Formen möglicher Erfahrung. Zs. f. Tierpsychol. 5, 235–409.

Lorenz, K. und N. Tinbergen, 1938. Taxis und Instinkthandlung in der Eirollbewegung der Graugans I. Zs. f. Tierpsychol. 2, 1–29.

Makkink, G. F., 1936. An attempt at an ethogram of the European Avocet (*Recorvirostra avosetta* L.) with ethological and psychological remarks. Ardes 25, 1–60.

Maxse, V., 1951. *Aegithalos caudatus roseus.* Proc. X. Internat. Ornithol. Congress Upsala (in press).

Meyknecht, J., 1941. Farbensehen und Helligkeitsunterscheidung beim Steinkauz (*Athene nocula vidalii* A. E. Brehm). Ardea 30, 129–174.

Nice, M. M., 1943. Studies in the Life history of the Song Sparrow II. Trans. Linn. Soc. New York 6.

Portielje, A. F. J., 1927. Ornitho-psychologische opmerkingen. Ardea 16, 20–22.

Pumphrey, R. J., 1948. The sense organs of birds. Ibis 90, 171–199.

Rand, A. L., 1941. Lorenz's objective method of interpreting bird behaviour. Auk 58, 289–291.

—— 1942. Nest sanitation and an alleged releaser. Auk 59, 404–409.

Shoemaker, H. H., 1939. Effect of testosterone propionate on behavior of the female canary. Proc. Soc. Exp. Biol. Med. 41, 299-302.

Thorpe, W. H., 1951. A review of learning in birds. Ibis (in press).

Thorpe, W. H., D. H. Wilkinson, R. J. Wojtusiak and others, 1949. A discussion on the orientation of birds on migratory and homing flights. Proc. Linn. Soc. London 160, Pt 2, 85–116.

Tinbergen, N., 1936. Field observations of East Greenland Birds I. The behaviour of the Red-necked Phalarope in spring. Ardea 24, 1–42.

—— 1939 a. On the analysis of social organisation among vertebrates, with special reference to birds. Amer. Midl. Natural. 21, 210–234.

—— 1939 b. Field observations on East Greenland Birds II. The behavior of the Snow Bunting (*Plectrophenax nivalis subnivalis* A. E. Brehm) in spring. Trans. Linn. Soc. N. Y. 5, 1–94.

—— 1940. Die Uebersprungbewegung. Zs. f. Tierpsychol. 4, 1–40.

—— 1942 a. De staartmees als bouwkunstenaar. De Lev. Nat. 46, 215–217.

—— 1942 b. An objectivistic study of the innate behaviour of animals. Biblioth. biotheor. 1, 39–98.

—— 1948 a. Social releasers and the experimental method required for their study. Wilson Bull. 60, 6–51.

—— 1948 b. Physiologische Instinktforschung. Experientia 4, 121–133.

—— 1951. The Study of Instinct. Oxford (in press).

Tinbergen, N., and D. J. Kuenen, 1939. Ueber die auslösenden und die richtunggebenden Reizsituationen der Sperrbewegung von jungen Drosseln (*Turdus m. merula* und *T. e. ericetorum* Turton). Zs. f. Tierpsychol. 3, 37–60.

Tinbergen, N., and A. C. Perdeck, 1950. On the stimulus situation releasing the begging response in the newly hatched Herring Gull chick (*Larus a. argentatus* Pontopp). Behaviour 3, 1–38.

Vanderplank, F. L., 1934. The effect of infra-red waves on Tawny Owls. Proc. Zool. Soc. London 505–507.

Weiss, P., 1941. Self-differentiation of the basic patterns of coordination. Comp. Psychol. Monogr. 17, 1–96.

Whitman, Ch. O., 1919. The Behavior of Pigeons. Carnegie Inst. Wash. Publ. 257,2, 1–161.

Yeagley, H. L., 1947. A preliminary study of a physical basis of bird navigation. Jour. appl. Physics 18, 1035-1063.

Zitrin, A., 1942. Induction of male copulatory behavior in a hen following administration of male hormone. Endocrinology 31, 690.

# Some Experiments on Imprinting Phenomena in Ducks

*Eric Fabricius*

*Institute of Freshwater Research, Drottningholm, Sweden*

The conception of imprinting originates from Lorenz (1935), who described how young grey lag geese recognize their parents. According to Lorenz the recognition of the parents is not innate in newly hatched young geese. During a short sensitive period the young follow the first living animal they see. After this the young geese will only follow animals of the same species, which evoked their first reaction to follow. For instance, if young geese, hatched in an incubator, are made to follow a human experimenter, they will after this refuse to be conducted by parent geese. The young geese are, according to Lorenz, imprinted to the human being.

In 1937 I proved that such an imprinting phenomenon also occurs in young tufted ducks, and in 1945 and 1946 I made some experiments with newly hatched tufted ducks (*Aythya fuligula*), eiderducks (*Somateria mollissima*) and shovelers (*Spatula clypeata*). As a detailed report of these experiments will be published later (Fabricius 1951), I shall now restrict myself to a short abstract of the more essential observations.

For the experiments the young were taken directly from the incubator in which they were hatched and, of course, every young bird could be used for one experiment only. The first task was to investigate the sign stimuli, which in the newborn bird release the reaction to follow a potential parent. The investigation began with an attempt to analyse the visual stimuli.

In the first series of experiments, 11 young tufted ducks were successively confronted with two stuffed adult females of the same species. The first dummy, which was immobile and mounted in a standing posture, never provoked any reaction in the young. The second model was mounted in a swimming attitude, and it could be drawn forward along the surface of the water. When immobile, it never evoked any reactions in the young, and when drawn forwards in some cases it evoked escape reactions, whilst in other cases the young did not pay any attention to it at all.

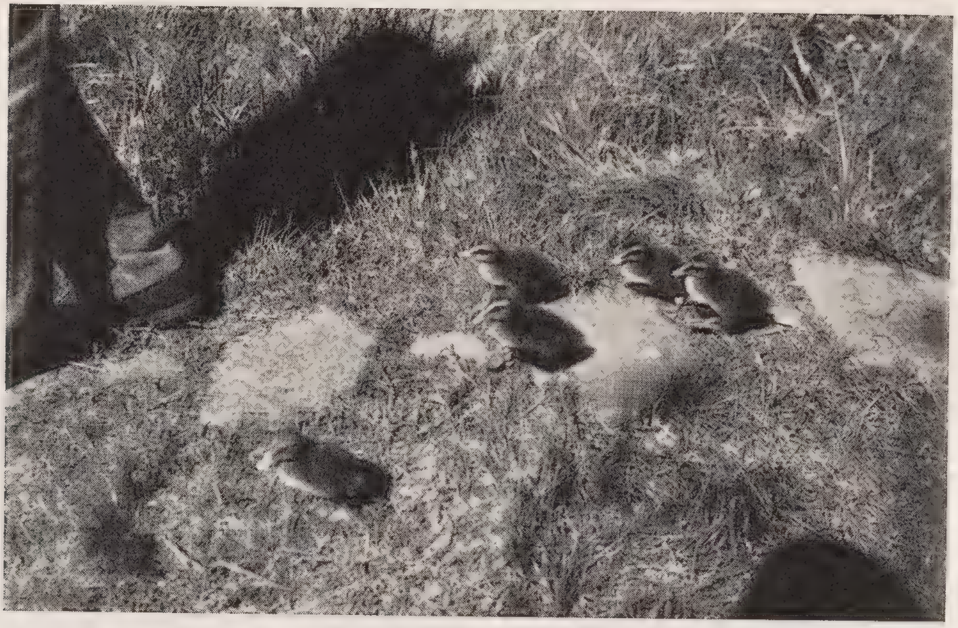


Fig. 1. Young eiderducks following the experimenter.

In a second series of experiments, 17 newly hatched tufted ducks were confronted with living ducklings of other species, namely either shovelers or eiders, which were some weeks older. 10 of the young tufted ducks crept to the older ducklings and followed them, in spite of the fact that the eiders and shovelers harassed and nipped them violently.

In a third series of experiments, 12 young tufted ducks were confronted with a human experimenter, sitting in silence in front of the young, and the same experiment was also made with 10 young eiderducks and 5 young shovelers. The shovelers, 2 of the eiders and 3 of the tufted ducklings ran to the experimenter and followed him. The birds, it is true, did not pay any attention to me as long as I was sitting quite motionless, but if I slowly stretched out my hand towards the young, they at once crept towards me, and if I moved in a direction away from them, they followed me.

The experiments with the models indicate that features of shape are not of great importance in releasing the following reaction of the young: nor does a gliding forward movement of a creature with exactly the shape of a swimming female duck. On the other hand, a moving human experimenter released the reaction in young tufted ducks, eiders and shovelers, and the sight of a some weeks older living eider or shoveler released it in newborn tufted ducks. Thus the most effective optical stimulus must be any quality of movement, characteristic of living vertebrates, but not occurring in a swimming model drawn forwards along the surface of the water. Most probably it lies in the fact that in living vertebrates several parts and limbs are moving in relation to each other in some characteristic way.

As mentioned, 8 of the young eiders did not run to me as long as I was silent. When I called them, however, they at once came to me and followed me. The same phenomenon was also recorded in 9 of the young tufted ducks. The call used was simply the Swedish verb "kom," repeated in a rapid series. Rhythmically the call had some similarity to the calls that Heinroth and Lorenz in German named "Unterhaltungslaut" or "Stimmfühlungslaut," that is the calls which in several duck species hold the members of a flock or a family together. The young always uttered their "Unterhaltungslaut" when following me.

The effect of the call alone, without additional visual stimuli, was proved in two experiments with tufted ducks. In each of these experiments newborn ducklings were put in a large box with opaque walls. The isolated young in the box uttered their characteristic distress call. Sitting outside the box, invisible to the birds, I uttered the "kom, kom, kom" call. The ducklings at once answered with their "Unterhaltungslaut" and crept towards me. Monosyllabic verbs other than "kom," when uttered in rapid succession, also released the action. In some of the dummy experiments a hissing sound was produced in the swimming model through a rubber tube. When a rapid series of short sounds was produced, the young in one case swam towards the model, but when no sound was produced they did not pay any attention to it. Long hissing sounds released escape reactions.

According to Lorenz (op. cit.), young mallards (*Anas platyrhynchos*) only follow a man if he imitates exactly the quacking of a female mallard. In 1948, however, I recorded that newly hatched mallards followed me when I uttered the "kom, kom, kom" call. Though rhythmically somewhat resembling the call of a female mallard, conducting its young, my call was by no means an exact imitation of a mallard's quacking. The experiments indicate that at least in newborn tufted ducks and mallards, rapid series of monosyllabic sounds release movements towards the sounds.

Sometimes it was necessary to repeat the calls for some seconds before the birds started to follow me, showing that the stimulus was successively accumulated until the level of reaction was reached. When I led the young, they always followed me better if I uttered the "kom, kom"-call, and this was the case not only in tufted ducks and mallards, but also in eiders and shovelers. Thus the visual and the auditory stimuli were added to each other, forming a typical example of heterogeneous stimulus summation (Tinbergen 1948).

In order to investigate the duration of the sensitive period, I made experiments with young tufted ducks, which had remained isolated in the incubator for different intervals after hatching. It appeared that the readiness to follow a potential parent was greatest in ducklings younger than 12 hours, and it rapidly decreased with increasing age. In ducklings more than 24 hours old I could not cause any following reaction towards me. The effectivness of visual stimuli was decreasing much more rapidly than that of auditory ones. When visual and auditory stimuli were presented together, they released a greater following reaction in older ducklings than did the exclusively visual stimuli. Auditory stimuli however, when presented alone, released the action in still older ducklings.

The decreasing readiness to respond positively to optical stimuli may partly depend upon the fact that the sight of a man, a bird or a moving model in some cases released escape reactions in ducklings older than 6 hours. In older young the readiness to respond with escape reactions to visual stimuli swiftly increased. When such a duckling ran away from me, it happened in some cases that it stopped if I uttered the "kom, kom"-call, and after I had repeated the call a little while, it might turn back and follow me.

After a duckling had followed a living being, it refused to follow beings of other species; that is, the imprinting was completed. For instance, the young tufted ducks, which at first had followed me, did not follow eiders or shovelers, and the tufted ducklings which followed the above-mentioned bird species did not follow me. On one occasion a wild adult female eiderduck discovered a group of eider ducklings which were imprinted to me. The female eider, which probably had lost her own young, swam close to my ducklings and tried to make them follow her. The young eiders, however, did not pay any attention to the female, but ran to me when I called.

In some cases a kind of incomplete imprinting occurred. The young tufted ducks followed me, but every sudden or rapid movement released escape reactions in them. This incomplete imprinting chiefly occurred in birds, which after hatching had remained isolated in the incubator for an extremely long time. When tufted ducklings did not follow me during their first 24 hours, it was not possible, except in one single case, to make them follow me later on.

Summing up, young tufted ducks, eiders, shovelers and mallards are not born without an "innate schema" (Lorenz, op. cit.) for the parent bird. On the contrary, they have a typical and well-developed innate releasing mechanism (Tinbergen 1939) for their instinctive reaction to follow a potential parent bird. The releasing mechanism responds to several visual and auditory sign stimuli, which are working together in a cumulative way. The sign stimuli, however, are so simple that the innate releasing mechanism is very unselective. During the first reaction, however, the mechanism becomes completed with conditioned elements, which makes it more selective. Thus, the duckling in imprinting does not attain a "releasing schema" for its reaction to follow a parent bird, but it only completes an already existing innate releasing mechanism.

## References

Fabricius, E., 1951. Zur Ethologie junger Anatiden. (With an English summary). Acta Zool. Fenn. 68: 1–178.

Heinroth, O., 1911. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. Verh. V. Internat. Ornith. Kongresses, Berlin, 1910, 589–702.

— 1924. Lautäusserungen der Vögel. Journ. Ornith. 72: 223–244.

Lorenz, K., 1935. Der Kumpan in der Umvelt des Vogels. Ibid. 83: 137–213; 289–413.

Tinbergen, N., 1939. On the Analysis of Social Organization among Vertebrates, with special reference to Birds. American Midland Naturalist 21: 210–233.

— 1948. Social releasers and the experimental method required for their study. Wilson Bulletin 60: 6—51.

# Inheritance and Learning in the Song of the Chaffinch, Fringilla coelebs L.

*Holger Poulsen*

*Zoological Gardens, Copenhagen*

Two males, taken from the nest when about 6 days old, were reared isolated in a room, where they could not hear other Chaffinches. The next year in the middle of January they began to twitter feebly, just as they had done in September. In the course of about a fortnight they sang loudly. They produced an imperfect version of the normal song consisting of short piping notes repeated in a quick rhythm followed by a hoarse buzzing. Thus there was an inborn disposition for the terminal flourish of the song, but it did not resemble the normal terminal flourish, which has to be learnt. It is interesting to know that this part of the song shows a geographical variation, thus I have heard a special song-variant consisting of an abrupt "chick" added to an otherwise normal song in Finland and at Uppsala, Sweden. In the Chaffinches reared in isolation the pitch and the rhythm were different from the normal song. Their song somewhat resembled that of the Greenfinch, *Chloris chloris* (L.) and the Lesser Whitethroat, *Sylvia curruca* (L.). Thus the inborn song is abbreviated and not so differentiated. In February the two Chaffinches were placed so that they could hear other Chaffinches at liberty. While the two Chaffinches were learning their song, a Linnet, *Carduelis cannabina* (L.) was in a cage next to them. They imitated some of its notes but when later on they also heard the Chaffinches outdoors they imitated the Chaffinches only. Thus there is an innate basis for the song and and innate disposition to adhere to and imitate only the song of their own species. Now the notes they had picked up from the Linnet disappeared and they retained their normal song and no longer imitated other birds. The two following years their song has been normal, even when they have been in an aviary together with other birds. Thus the song is partly innate and partly learnt as is also stated by Hagen (1923) and Heinroth (1926).

But when does the Chaffinch learn its song? At the beginning of September I caught two young males. These young birds were hatched in June and had heard Chaffinch-song until the end of July, so possibly they would have the normal song next spring? They were kept isolated in a room, where they could not hear other Chaffinches. If later on they had a normal song, they must have learnt it already when young. At the beginning of the following year they began their song, which was faint and imperfect as the song always is at the beginning. When later on they sang aloud it turned out that their song was exactly the same as the song of the birds reared in isolation from an age of one week. These two birds were kept isolated until the beginning of May. They were then placed outdoors each one in its own cage and were now constantly hearing Chaffinch-song, but they never learned it. Nor did they have the normal song the following year. Thus the acquired part of the song seems to be learnt by imitation in the first spring of the young birds' life, when they begin to sing themselves, and in this period only, as Promptoff (1930) also supposed. Later the song has become fixed and is unalterable. This has already been stated by Pernau (1716 cited in Stresemann 1947).

As direct experiments on the influence of testis hormone on bird song have only been made in very few cases and not with wild birds with a typical song, I tried to find the causal relation between song and testis development. Male sex hormone was injected into females and males when not in a reproductive mood. In December two adult males got injections of testosterone propionate[1] in their chest muscles (5 mgms every 3rd–4th day, 25 mgms in all). After three injections (6th day of treatment) they began to sing feebly and imperfectly. After the fourth injection (8th day of treatment) their song was fully developed. Following the fifth injection (15th day of treatment) the song was loud and perfect. Thus the imperfect song of the Chaffinch in the beginning of the song period is due to the initial effects of the male sex hormone. The song stopped 5–6 days after the last injection. It is known that a kind of song is sometimes heard from females at liberty, and two adult females were singing feebly and twittering after 6 injections of 5 mgms testosterone propionate (23rd day of treatment). The notes were hoarse and buzzing and did not at all resemble the song of the adult males. These females did not produce the different call-notes typical of the male in spring.

After sex hormone treatment the male birds reared in isolation produced the notes typical of the male in a reproductive mood. So these notes are innate, even: uid (German: Regenruf) characteristic of the mated male in spring is inborn. As is known there are different geographical variants of this note. In Denmark I have heard two variations: ryd and uid. Still more variations within rather small areas are mentioned for Germany by Sick (1939).

---

[1] I am indebted to Mr. E. Wilkens (Ciba, Copenhagen) who supplied me with the hormone.

While in the Chaffinch the song is partly innate and partly acquired, it is quite different in other species. In the Tree-Pipit, *Anthus trivialis* (L.) and the Reed-Bunting, *Emberiza schoeniclus* (L.) birds reared in isolation have a perfect song. In the latter species the song-variants may be due to inheritance. Other species have to learn their song as is the case with the Linnet, *Carduelis cannabina* (L.); only the call-notes, which are a component of the song of this species, are inborn. The call-notes of the Chaffinch and the Reed-Bunting are also inborn.

## References

HAGEN, W., 1923. Ist der Gesang des Buchfinken angeboren oder erlernt? Orn. Monatsber. 31, p. 52–54.

HEINROTH, O. und M., 1926. Die Vögel Mitteleuropas. 1.

PROMPTOFF, A. N., 1930. Die geographische Variation des Buchfinkenschlags in Zusammenhang mit etlichen allgemeinen Fragen der Saisonvogelzüge. Biol. Zentralblatt 50, p. 478–503.

SICK, H., 1939. Dialektbildung beim Regenruf des Buchfinken. Journ. Ornith. 87, p. 568–592.

STRESEMANN, E., 1947. Baron von Pernau, pioneer student of bird behavior. Auk. 64, p. 35–52.

# Vögel erlernen unbenannte Anzahlen

*O. Koehler*

*Zoologisches Institut, Freiburg i. Br.*

Vor 27 Jahren begann mein damaliger Schüler W. Fischel Tauben auf gesehene Anzahlen zu dressieren; seit 17 Jahren mit nur dreijähriger Nachkriegsunterbrechung sind wir weiter am „Zähl"-Problem beschäftigt. Veröffentlicht wurden bisher die Versuche von O. Müller, H. Wachholtz, W. Arndt an Tauben, von E. Marold an Wellensittichen, von K. Schiemann an Dohlen, von mir am Kolkraben Jakob und erwachsenen Menschen unter Bedingungen, die ihnen das Zählen in Worten unmöglich machten. In erhaltenen Protokollen harren der Veröffentlichung Versuche an 12 weiteren Kolkraben und einem Graupapagei aus den letzten Kriegsjahren in Königsberg; in Freiburg laufen neue Versuche an Elstern, Amazonen, Graupapageien und Eichhörnchen, sowie an Kindern, die noch keine Zahlwörter gebrauchen, in Frankfurt a. M. an Affen.

Von mehr als 3 Kilometern Film, die die meisten der veröffentlichten Versuchsarten belegten, ist wenig mehr erhalten als das, was Sie sogleich sehen werden. Wieviel Einzelversuche bereits vorliegen, vermag ich im Augenblick nicht zu schätzen, vermute sie aber hoch in den Hunderttausenden.

Immer wieder hörte ich die Frage, ob soviel Arbeit eine so unbiologische Fragestellung lohne. Tatsächlich wüsste ich, trotz allen Jägergeschichten von der Krähenhütte usw., keine sichere Beobachtung zu nennen, die bei einem Wildtier praktisches Zählen wenn auch nur bis 3 bewiese. Aber ein jedes Experiment ist an sich unbiologisch; nur die Fragestellung, der es dient, sollte allerdings biologisch sein.

Es geht hier um den Ursprung der menschlichen Sprache, des einzigen Vermögens also, das der Mensch vor den Tieren voraus hat und das allein ihm die durchaus neue und höchste Schicht seines Wesens, seine Geistigkeit eröffnete.

Bekanntlich gibt es keine Definition des Lebens. Allein seine Merkmale können wir aufzählen, deren keines fehlen darf, soll von Leben die Rede sein. Für die meisten dieser Vermögen finden wir mehr oder weniger Vergleichbares im Unbelebten, etwa die Flamme als Symbol des Stoffwechsels bei relativer Formkonstanz, aber niemals alle zusammen; und deshalb bleibt zwischen Leben und Unbelebtem die Grenze scharf.

Ebenso kennen wir tierische Vorstufen unserer Sprache, Sprachwurzeln, wie Gehlen sagt: 1) das akustisch-phonetische Vermögen der Lautnachahmung seiner selbst vielleicht bei jedem Vogel, des Artgenossen bei vielen, auch fremder Artgesänge bei den Spottvögeln, nahezu beliebiger Laute einschliesslich menschlicher Sprachlaute bei Krähenvögeln und Papageien. 2) Situationsgebundenheit bestimmter Laute: angeboren vielleicht zwei verschiedene Warnrufe für Boden- und Luftfeind bei Hühnervögeln, erworben wenn z. B. mein Graupapagei Hallo rief, sowie jemand den Telefonhörer abhob, ,,Nu auf Wiedersehen", wenn einer zur Tür hinausging. Einzeln erlernte Wörter 3) kontaminierte er zu einem neuen; aus ,,Kuhks" und ,,Kuckuck" wurde ,,Kuducks", und er gewöhnte sich, allabendlich solange Kuducks zu schreien, bis wir das Licht ausdrehten, ihn zudeckten und allein liessen. Somit 4) bedeutete endlich sein erlerntes Kuducks im Ergebnis dasselbe wie der menschliche Befehl: bringt mich zu Bett. 5) Die soziale Mitteilungsfunktion angeborener Laute und Instinktbewegungen ist durch zahllose Beispiele belegt; der Schwänzeltanz der Biene teilt sowohl die Art der verheissenen Tracht (Duft) als auch Richtung und Entfernung des Fundortes erstaunlich genau mit, wobei abermals die Symbolfunktion (eine der Hauptsprachwurzeln Gehlens) klar liegt: Genau senkrechtes Aufwärtsschwänzeln auf der senkrecht stehenden Wabe befiehlt Ausflug sonnenwärts, Abwärtsschwänzeln Ausflug sonnenabwärts, Winkelabweichungen werden nach einmaligem Mittanzen auf knapp 5° genau behalten, vom optischen auf den Schweresinn bezw. umgekehrt transponiert. Die Aufzählung der Wurzeln ist damit nicht erschöpft.

Die Summe der Wurzeln macht noch keinen Baum. Keine Tierart verfügt über alle Wurzeln zugleich, und schon deshalb bleibt, wie die Grenze zwischen Leben und Unbelebtem, auch die zwischen allen (nichtsprechenden) Tieren und dem allein sprechenden Menschen scharf. Aber das täglich sich wiederholende Wunder der Entwicklungsgeschichte (man denke an das Heranwachsen der Pflanze dank autotrophem Stoffwechsels und an das Bewusstwerden des Menschenkindes), mahnt uns, dort wie hier zugleich der Stammesgeschichte nachzudenken.

Zur Frage der Urzeugung weiss die Naturforschung einstweilen nur zu sagen, dass es sie heute nicht gibt. Der Physiologe Jordan nannte sie die unsinnigste aller Hypothesen. Heute fassen manche neuen Mut, ohne aber auch nur im geringsten zu überzeugen. Nur innerhalb höchster Lebewesen sahen wir bisher das Virus sich vermehren. Man wird ebensowenig im Chromosom, welches Th. Boveri in seinem Sinne gewiss mit Recht eine Individualität nannte, eine stammesgeschichtliche Vorstufe der Zelle sehen, wie heute im Virus eine solche des Chromosoms, geschweige der Zelle.

Liegt das Problem der sogenannten Menschwerdung, also der Herkunft der Sprache ebensoweit jenseits der heutigen naturwissenschaftlichen Leistungsgrenzen?

Es ist gewiss nicht von ungefähr, dass noch kein Buch über die Psychologie des menschlichen Neugeborenen geschrieben wurde. Es schreit bei Hunger und Kälte, es trinkt sich satt und schläft weiter, genau wie ein saugendes Kätzchen. Sein noch unkoordinierter Blick sagt uns nichts. Bald beginnt des Kind zu lächeln, etwas später neue Laute zu formen. Ob auch ein Kaspar-Hauser-Säugling Lallmonologe komponieren würde, ob auch das vom Ei ab schallisolierte Singvogeljunge einmal zu ,,dichten" beginnen würde, das wissen wir noch nicht.[1] Beim normal in menschlicher Gesellschaft aufwachsenden Säugling erwacht der Klangnachahmungstrieb zu seiner Zeit. Die Erwachsenen sprechen vor, behutsam gemäss der jeweiligen Fassungskraft dosiert, ganz wie zum Papagei, nur meist situationsgebundener, z. B. ma ma ma in Anwesenheit der Mutter, ada ada beim Abschied. Dort wie hier sind die Wörter zweifellos rein erlernt; das beweist ja schon die Vielzahl der Muttersprachen und Dialekte. Hat aber das Menschenkind erst einmal einige wenige Wörter nebst ihren noch so unscharf, ja im Sinne der Erwachsenen oft falsch abgegrenzten Situationsbindungen (,,Bedeutungen", ,,Wortsinn") erfasst, so spricht es eines schönen Tages plötzlich höchst überraschenderweise seinen ersten Satz, etwa mama ada. Es reihte seine zwei getrennt erlernten Wörter aneinander, nicht bedeutungslos, wie die Singdrossel ihre Motive — hoffentlich tun wir ihr nicht unrecht — sondern vielmehr sinnvoll, tatsachentreu: Gerade als eben die Mutter weg war, da sagte das Kind mama ada. Das Kind braucht nicht Satzlehre, Grammatik und Wahrheitsliebe zu lernen, um seine ersten Wahres aussagenden Sätze zu bilden; nein, dieses Vermögen ist ihm angeboren, und der ,,klügste" Papagei hat solches meines Wissens noch nie geleistet. Das ist die Kluft zwischen dem Menschen und allen Tieren, und heute ist sie durchaus unüberbrückt. Aber wie die rezente Kluft zwischen Bär und Mungo uns nicht hindert, nach einem beiden gemeinsamen carnivoren Ahn zu suchen, genau so dürfen wir uns über die Stammesgeschichte des Menschen Gedanken machen; und da die ausgegrabenen Zähne, Kiefer- und Schädelreste uns nicht verraten, wer erst lallte und wer schon sprach, so fällt der Blick auf die Dienste der Vergleichenden Verhaltensforschung, nachdem die Vgl. Anatomie und Vgl. Physiologie, die Vgl. Entwicklungsgeschichte, die Genetik usw. usw. schon so vieles beigetragen haben.

---

[1] Anm. bei der Revision. Heute (30.9. 51) wissen wir es. Solch ein Dorngrasmückenjunges dichtet voll artgemäss (F. Sauer, unveröffentlicht).

Die Vgl. Verhaltensforschung aber lehrt, wie schon gesagt, dass wir, von den Artunterschieden abgesehen, mit den Tieren gemeinsam haben die Sinne, ja die gesamte Reizphysiologie, insonderheit die Gangarten als zentralnervöse Automatismen, die Orientierung in Raum und Zeit, die Instinktbewegungen nebst den sie auslösenden angeborenen Schematen, die Stimmungen, die Affekte, das Lernvermögen auf der Grundlage des Gedächtnisses, weithin vergleichbare Domestikabilität. Vor allem aber bilden höhere Tiere vermöge aller aufgezählter Vermögen die Aussenwelt innerlich — gewiss artverschieden, immer aber derart ab, dass jedes sich in ihr zurechtfindet, sich lebenserhaltend mit ihr auseinandersetzt, in sie planvoll hineinzuhandeln vermag. Sie bilden nachweislich „anschauliche", allgemeiner gesagt „sensorische" Vorstellungen, Begriffe, und Urteile, anders ausgedrückt, sie „denken unbenannt". Und da auch wir Menschen das, was wir sagen wollen, noch vor der Wortfassung bereits wortlos wissen, so glaube ich, eben diese vorsprachlichen Vermögen, eine innere Anschauung der Aussenwelt wie auch des eigenen Innenlebens zu bilden, die die Tiere im Lauf ihrer Stammesgeschichte sich geschaffen und auf uns vererbt haben, ich sage diese vorsprachlichen Vermögen machen das grosse Rätsel begreiflicher, warum schon der erste selbsterfundene Satz des Kleinkindes grundsätzlich ebenso tatsachentreu Verlässliches aussagen kann wie der Naturforscher, der seine Beobachtungen in die raffiniertest verfeinerte Gesetzesaussage fasst. Unsere Menschenworte passen zu unserer Aussen- und Innenwelt deshalb, weil wir vorsprachliche Inhalte eineindeutig zu benennen gelernt haben. Die vorsprachlichen Inhalte aber passen zum Aussen- und Innengeschehen ihrer tierischen wie menschlichen Bildner genau so, wie das Auge zum Sehen, das Hirn zum Integrieren von Sinnesempfindungen und Verhaltensformen, wie der Flügel zur Luft, die Flosse zum Wasser, wie jedes Organ zu seiner Funktion, und aus demselben historischen Grunde: dank einem vielleicht anderthalb Milliarden Jahre langen Anpassungsgeschehen in der Auseinandersetzung der Tiere mit ihrer Umwelt, wobei Mutation, Vererbung und Auslese des jeweils Passendsten wesentlichste Evolutionsfaktoren waren.

Der Sinn unserer speziellen Arbeit war es, eben diese Behauptung an einem Beispiel möglichst genau zu belegen. Wir suchten nach tierischen Vorstufen menschlichen Zählens.

Von der höchst umfangreichen Literatur über die Entwicklungsgeschichte kindlichen Zählens kenne ich erst spärliche Bruchstücke. Vieles aber scheint hier kaum verwendbar, schon weil z. B. manche Beobachter sich nicht einmal dafür interessiert zu haben scheinen, ob ihre Versuchspersönchen bereits Zahlwörter kannten, und wenn ja, welche. Ich erwähne nur eine eigene Beobachtung. Ein knapp vierjähriges Mädchen hatte ohne Wissen der Eltern bei einem Besuch einer verlässlichen alten Freundin die Zahlwörter von 1 bis 8 in rechter Folge aufzusagen und die dazugehörigen Ziffern zu lesen gelernt. Kurz darauf überraschte sie die Mutter an der Trambahnhaltestelle durch den Satz: ,,Da kommt die Drei und hat 3 Wagen, das passt zu dem, was sie ist.“ Die Nachfrage ergab mit Sicherheit, dass die Freund in nichts mit dem Kinde abgezählt, nichts über Zahlengebrauch und das Zahlenwesen gesprochen hatte. Nichts mehr war geschehen, als oben mitgeteilt. Der Vorfall zeigt, dass — sind die Zahlwörter erst einmal da — ihr Gebrauch sich von selbst versteht, somit dem normalen Kinde angeboren ist, als Spezialfall des oben bereits besprochenen Angeborensein des sonstigen, allgemeinen Wortgebrauches. Hilfsschulkinder dagegen, die dressurartig gelernt haben, 3 Klötzchen in 3 Löcher zu stecken und dazu 1, 2, 3 zu sagen, können darum noch längst nicht drei Äpfel zählen; es kann Jahre brauchen, bis ihr Zählen objektunabhängig wird. — ,,Da kommt die Drei“ — das war die gelesene Ziffer. ,,und hat 3 Wagen“ — die hat sie abgezählt. ,,Das passt zu dem, was sie ist“ — das wäre die praktische Anwendung des absoluten Begriffs der benannten Zahl, als des Einzigen, bereits völlig Unanschaulichen, was Ziffer und Anzahl gemeinsam haben.

Keiner unserer Vögel hat jemals auch nur annähernd Vergleichbares erlernt. Sie zählen nicht, denn es fehlen ihnen die Zahlwörter. Wohl aber haben sie alle gelernt, unbenannte Anzahlen erstens zu sehen, und zweitens sie abzuhandeln.

Das erste der beiden vorsprachlichen Vermögen erlaubt ihnen, gleichzeitig nebeneinander gebotene Mengen im optischen Simultanvergleich allein nach der gesehenen Anzahl ihrer Glieder zu unterscheiden.

Wir bieten z. B. der Taube auf einem Pappstreif einerseits 2, gegenüber 3 Körner und scheuchen sie von den dreien fort; die 2 darf sie fressen, wenn sie sich ihnen zuerst zuwandte. Der Versuchsleiter ist hinter einer Trennwand unsichtbar, zum Scheuchen dient eine Maschinerie, die ganz oder gar nicht losgeht. Im ,,Spontanversuch“ — nur solche wurden gefilmt, stets nur von statistisch voll gesicherten Lösungen — ist sie ausgeschaltet; der Vogel zeigt völlig unbeeinflusst, ob er etwas gelernt hat und was. Die beste Taube kam bis hinauf zu 6 Körnern gegen 5; dies vergass sie freilich meist wieder über Nacht und kam dann schnell wieder darauf; einfachere Aufgaben behielt sie ohne Nachüben bis zu 14 Wochen. Dieselbe Taube versagte bei der gewiss leichter scheinenden Aufgabe, 2 von 3 Tuschpunkten auf Schälchendeckeln zu unterscheiden; nur über „volle Figurenhilfe" lernte sie es endlich und war ausserstande, das Lösungsprinzip aufs Körnerbrett zu übertragen. Zwischenziele und gleichzahlige primäre scheint sie nicht gleichwerten zu können. Anders die Dohle, die sogleich figurenunabhängig, also bei völlig beliebig wechselnder Anordnung 3 gegen 4 Tuschpunkte auf Schälchendeckeln zu unterscheiden lernte. Als man ihr plötzlich Mehlwürmer statt der Punkte auf die beiden weissen Deckel legte, hob sie nicht mehr Deckel ab, wie zuvor, um darunter nach dem versteckten Köder zu suchen, sondern frass die 3 Mehlwürmer und liess die 4 liegen. Auch das Prinzip der Musterwahl, statt der bisherigen Dressuren auf etwas Bestimmtes, bei dauernd wechselnden Darbietungen „Gleiches zu Gleichem zu ordnen", haben Dohlen erfasst. Geboten waren 2 Deckelschälchen mit z. B. 2 und 4 Punkten. Trug der davorliegende Musterkarton gerade 2 Punkte, so öffnete sie den Zweipunktdeckel; trug das Muster 4 Punkte, dann den mit 4 Punkten. Am Ende wechselten die Muster ständig von 2 bis 5, ebenso auch Lage und Grösse der Punkte. Mein Kolkrabe Jakob gewann rasch Überblick über nicht weniger als 5 Schälchen und leistete an ihnen Musterwahl von 3 bis 7 Reisszwecken in jeweils wechselnden Lagen, ebenso von 2 bis 6 Plastilinflecken von ständig wechselnder Gestalt (Umriss), Lage und Grösse (Grenzverhältnis der Flächeninhalte der „Punkte" 1: 50). Dass derartige Aufgaben bis zu 11-mal hintereinander an erster Stelle richtig gelöst wurden, bei ständig wechselndem Muster, was vorkam, dafür ist die Zufallswahrscheinlichkeit astronomisch gering. Den Einwand, der Rabe habe den Köder im Schälchen, dessen Deckel die gleiche Punktzahl trug wie das Muster, gerochen, schlossen Kontrollversuche ohne jeden Köder oder mit 5 gleichbeköderten Näpfen aus. Auch hier hat Jakob allein den richtigen Napf geöffnet, selbst dann, wenn ich ihn im grossen, dichtverwachsenen Garten stundenlang mit seiner Versuchsanordnung allein liess. Kam ich zurück, so hatte er allein den dem Muster entsprechenden Napf geöffnet und geleert, alle vier anderen waren unberührt. Hier hilft auch nicht die Zuflucht zur „Gedankenübertragung". — Andere Kolkraben haben an 5 Schälchen recht glatt das Prinzip erfasst, immer die eine vom in sich anzahlgleichen Rest allein abweichende Punktanzahl zu wählen, also wenn z. B. erst 44434, dann 34333 geboten wurde, im ersten die 3, im zweiten die 4, und so fort.

Mehreren 100 Menschen boten wir dieselben Aufgaben als Lichtbilder, die zu kurze Zeit sichtbar blieben, als dass man die Punkte hätte auszählen können, jedoch nicht kürzere Zeit, als die Vögel sie sich zur Betrachtung nahmen. Fast keiner leistete mehr als Kolkrabe und Graupapagei, deren obere Grenze des ersten Vermögens, Punktgruppen (die sich um nur je eine Einheit unterscheiden) allein nach der gesehenen Anzahl ihrer Glieder zu wählen, bei der 7 liegt. Die Mehrzahl der Menschen fand ihre Grenze, wie Dohle und Sittich, bei der 6, nicht ganz wenige, wie die Taube, bei der 5.

Das zweite Vermögen ist unanschaulich und sukzessiv. Es gilt zu erfassen, wie oft ein gleichartiges Ereignis (z. B. Köderaufnahme) sich wiederholt.

Die beste Taube lernte, von 7 bis 13 gleichabständigen Körnern immer nur 6 zu fressen. Den Pickrhythmus zerstörten wir in sehr verschiedener Weise, am gründlichsten wohl, zugleich mit dem Figureneinwand, der, wenn gegen das Fressen ,,vom grossen Haufen" gerichtet, eigens widerlegt wurde, indem wir in von 1 bis 60 sek regellos wechselnden Zeitabständen harte Erbsen einzeln aus einem Rohr in eine Schale laufen liessen. Sie sprangen darin so rasch herum, dass eine Taube nach derselben Erbse bis zu 14 mal picken musste, ohne sich deshalb zu ,,verzählen". Ein alter überaus scheuer Kolkrabe begann mit der Aufgabe, an einer Schälchenreihe solange Deckel abzuheben, bis er 7 Köder gefunden hatte, die in ständig wechselnden Verteilungen darin lagen. Waren z. B. alle 7 beisammen im ersten Schälchen, so öffnete er nur dieses; lag in jedem der ersten 7 Schälchen je ein Köder, so blieb der achte Deckel als erster unberührt, und so fort. Er hat sie glänzend gelöst.

Von solchen Aufgaben lernten Tauben gleichzeitig zwei, Dohlen bis zu 4 gleichzeitig zu beherrschen. Wellensittiche nahmen 2 Hirsekörner vom grossen Haufen, wenn man dyo dyo . . . sagte bezw. klingelte, und 3 zu treis treis . . . bezw. zum Summer. Dohlen hoben weisse Deckel ,,auf 5", rote auf 4, grüne auf 3 und schwarze auf 2 Köder ab.[1]

Die obere Grenze des zweiten Vermögens war bisher für jede Vogelart die gleiche wie beim ersten, also wiederum 7 bei Kolkrabe und Graupapagei, 6 bei der Dohle und so fort. Noch nicht zählende Kinder leisteten bisher deutlich weniger, ein 16-Jähriger kam unter harten Bedingungen, die sein Mitzählen ausschlossen, nicht über die 6 hinaus.

Diese Grenzübereinstimmung beider Vermögen, des simultanen und des sukzessiven, bei bisher 5 Tierarten und dem Menschen, sofern wir ihn auf unbenannte Anzahlen reduzieren, kann unmöglich Zufall sein. Sie scheint mir den Arbeitsaufwand zu lohnen, indem sie zeigt, dass wir diese beiden vorsprachlichen Vermögen mit höheren Tieren teilen, sie mithin von ihnen haben. Es liegt auf der Hand, dass ohne sie, ohne die sinnlichen Vorformungen unserer Begriffe wie mehr/weniger, länger/kürzer, schwerer/

---

[1] Ein Graupapagei handelte je nach der gehörten Anzahl (a-rhythmische Flötentöne, Metronomschläge) an der wechselnd beköderten Schälchenreihe auf 2, 3 oder 4 (L. Braun, unveröffentlicht).

leichter usw., die alle ebenso höheren Tieren eignen, ganz gewiss der Mensch niemals aufs Zählen, also auf die Schaffung von Zahlwörtern gekommen wäre.

Nicht nur die unwissentliche Zeichengebung, der die Lehrmeister der ,,zahlsprechenden, klugen“ Hunde und Pferde zum Opfer fielen, sondern darüber hinaus alle aufgabenfremden Schlüssel, alle Aussenmerkmale also, die dem Vogel das Signal zum Einstellen seines Handelns hätten geben können, hoffen wir ausgeschaltet zu haben. So kann es nur ein Inneres gewesen sein, und das zwingt uns zu psychologisieren. Welcher innere Vorgang sagt dem dressierten Vogel, dass das Öffnen weiterer Deckel sich nicht mehr lohnt, dass dies das letzte erlaubte Korn war, wo doch die bereits verbotenen seinen Schnabel, der eben das letztzuständige Korn aufpickt, buschstäblich berühren (Sittich)? Wir nannten es den ,,inneren Vorsatz, auf x zu handeln“.

Zur verschwenderischstmöglichen Annahme, die Vögel zählten wirklich auf ihre Weise, d. h. sie hätten qualitativ verschiedene, eineindeutig gereihte innere Marken gebildet, etwa wie Kinder am Abzählvers mitdenken, was benannten Zahlen, also echtem Zählen gleichkäme, besteht kein Anlass, da jede Andeutung von echtem Zahlenverständnis durchaus fehlt. Rückdressur auf eine früher bereits erlernte Aufgabe kann schwerer sein als ihr Ersterlernen. Fernerstehende könnten etwa bei Jakob an ein ,,Lernenlernen“ denken, da sich die Aufgaben immer schwieriger gestalteten und doch gelöst wurden. In Wahrheit aber kann manch eine schwere Aufgabe in Erstdressur ebenso rasch gelöst werden, wie nach vorsichtiger Vorbereitung durch leichtere. Höchstbezeichnend ist gerade auch für ihn, wie ihm das Prinzip der Musterwahl um so häufiger vorübergehend entgleitet, je schwerer die Darbietungsformen sind. Genau so erging es zwei älteren Kindern, die ich ganz wie Jakob aus seiner ihnen schweigend vorgelegten Versuchsfolge das Lösungsprinzip erraten liess. Beiden ist es zweifellos sehr früh aufgegangen und, nach drei aufeinanderfolgenden richtigen Lösungen, die gewiss kein Zufall waren, sofort wieder entglitten; es war unbenannt geblieben. Sowie sie es aber erst einmal in Worte gefasst hatten — und eben das kann Jakob nicht — sass es eisern fest.

Die bescheidenstmögliche Annahme, die des Erlernens unbenannter Anzahlen, bedeutet, dass die inneren Marken, an denen der Vogel entlanghandelt, alle qualitativ gleich sind. Z. B. könnte er für 1 sich einmal, für 2 zweimal innerlich zunicken und so fort. Das wird als unvollendetes Intentionspicken tatsächlich manchmal äusserlich sichtbar. Der Taubenfilm zeigt mehrfach nach vollen Pickschlägen auf erlaubte Körner sehr deutlich den kurzen Luftschlag gegen das erste verbotene, das programmässig liegen bleibt. Der einzigartige Fall einer Dohle blieb leider unverfilmt. Sie sollte an der Schälchenreihe Deckel auf 5 Köder öffnen; die Verteilung lautete 1, 2, 1, —, 1. Als sie die ersten drei Deckel geöffnet und 4 Köder entnommen hatte, ging sie davon. Als Schiemann gerade protokollierte: falsch, ein Köder zu wenig, da kam sie wieder, nickte im Vorbeigehen an den drei ersten offenen leeren Schälchen jedem sooft zu, wie Köder darin gewesen waren, öffnete das leere vierte, dem fünften entnahm es den letzten Köder und ging endgültig ab, ohne den Rest der Reihe eines Blickes zu würdigen.

Allein die Versuche mit vorzeitigem Scheuchen bei Wellensittich und Dohle könnten die sparsamstmögliche Deutung unbenannter Anzahlen zu bescheiden erscheinen lassen. Wenn eine Dohle in der noch laufenden Dressur auf 7, die nicht voll erlernt wurde, unverhofft schon beim dritten Köder gescheucht, in vielen unmittelbar folgenden Spontanversuchen durchschnittlich recht genau auf 3 handelt und erst nach einer halben Stunde, obwohl doch die Strafe hartnäckig ausbleibt, auf die hohe Dressurzahl zurückfällt, so gibt das zu denken. Wie kann eine von 6 gleichwertigen Marken durch einmalige Akzentuierung so eindeutig werden, und das für so lange Zeit? Da alles andere strikt gegen benannte Anzahlen spricht, haben wir uns mit der Hilfsannahme vom Valenzcrescendo der Scheuchangst begnügt, das über der Reihe gleichartiger Marken liegen möchte. Es bleibt bei den unbenannten Anzahlen.

Endlich fragten wir, ob ein Vogel, obwohl ihm mit dem Namen gewiss auch der Begriff der benannten Zahl fehlt, der ja allein das erste mit dem zweiten Vermögen eint, nicht wenigstens lernen könne, beide durch einen Lernakt miteinander zu verknüpfen.

Gesehene Anzahlen abzuhandeln hat eine Dohle nach vielen Fehlschlägen doch gelernt: aus einem Kreis von Mehlwürmern nahm sie zwei, wenn im Zentrum zwei Tuschpunkte sichtbar waren, und zu 4 Tuschpunkten vier Würmer. Eine Blaustirnamazone hob an der wechselnd beköderten Schälchenreihe Deckel auf 2 Köder ab, wenn sie 2 grössen- und formverschiedene Plastilinflecken gesehen hatte, bezw. auf 3 nach Anblick von 3 Flecken.

Und auch das Gegenstück, abgehandelte Anzahlen zu sehen, ist Fräulein L. Braun inzwischen geglückt. Eine Amazone hob von 5 Napfdeckeln nur den ab, der ebensoviele Reisszwecken trug, wie sie vordem Körner auf dem Musterdeckel gefressen hatte (1, 2, 3, 5 oder 7). Mit grössen- und formverschiedenen Deckelflecken glückte noch die entsprechende Dreifachwahl auf 1, 3 und 5. Wenn endlich die abzuhandelnden Körner der Schälchenreihe zu entnehmen waren, gelang Zweifachwahl auf 1 und 3.

Wir haben 2 vorsprachliche Vermögen als gemeinsamen Besitz von Mensch und Tier kennen gelernt, die nebst manchen anderen den Menschen aufs Zählen gebracht haben müssen. Was Tiere ihm unbenannt übermachten, das brauchte er nur noch zu benennen. Die Eignung dieser unserer Zahlen zur Grundlage der Algebra, darüber hinaus die Anwendbarkeit der Mathematik als Deuterin natürlicher Gesetzmässigkeit, die jederzeit realisierbare Voraussagen möglich macht, scheint letzten Endes zurückführbar auf die Stammesgeschichte tierischer „Weltabbildungsapparaturen" (K. Lorenz), wie denn wohl selbst der abstrakteste menschliche Gedanke im Anschaulichen wurzelt. Der methodische Weg aber zur Verallgemeinerung vom Beispiel der Stammesgeschichte des Zählens auf die der Sprache insgesamt scheint vorgezeichnet.

# The Display of the Satin Bowerbird, Ptilonorhynchus violaceus Vieill.[1]

*Dieter Burckhardt and Joseph A. Murnin*

*Zoological Institute,*
*Basel, Switzerland*

*Bethlehem, Ps., U. S. A.*

Last summer we had an opportunity of studying in the Bronx Zoo at New York the display of a Satin Bowerbird male and to make some tests concerning his selection of colours. It may be generally known that Satin Bowerbird males build on the soil some kind of a display bower from twigs, which they chiefly decorate with blue objects. Our tests have once more confirmed their preference for blue colours. Gray, for instance, reflecting the same quantity of light as blue was not taken into consideration. Much has been written about the building and its being adorned with blue objects. Unfortunately anthropomorphic ideas often seem to have diverted the observers' thoughts. We shall now try to give you an idea of the Satin Bowerbirds' breeding cycle according to what we learned from the papers written on the subject as well as from our personal experiments. We shall then go into the question of the origin of the display motions.

In the non-breeding season the Satin Bowerbirds live in smaller or larger flocks. At the beginning of the breeding season, i.e. in September, every adult male will build a bower. After which he will sing and dance either near the bower or in the foliage of some tree near by or else he will fly around mostly with some blue object in his bill looking for some female there. As soon as he finds her he will sing and court her showing her some blue object. Most probably the females will come near the bower by themselves. It may be said schematically that two different display attitudes on the part of the male may be observed, which correspond to a higher and a lower degree of excitement. In the former case—which manifests itself by the stooping of the female as an introduction to mating—the male will hold his plumage tight to his body with his neck stretched. In the latter case his plumage, particularly on the head, will be ruffled up, while the wings are lowered. The male will then show the female some blue object or some leaf, crouching down in front of the female with his head bent and his tail raised. That may last a full minute. At the same time the male will not stop singing. Of course there may be medium stages between the two attitudes. The mating seems to take place near the bower. The nest is built on some tree by the female only. The nest consists of twigs lined with leaves. Only the female is incubating and raising the young. During this time the male goes on displaying. Most probably he will try to make various other females come to his bower, mating them there. He seems to defend a certain territory round about the display ground.

---

[1] This is a preliminary report of a series of studies supported by the Behaviour Research Fellowships of the New York Zoological Society at the Zoological Park, New York City, during the summer of 1949. The report was illustrated with film and sound record.

We now come to the question of the origin of the males' display patterns. A survey of the reproductive biology of the nidicolous birds, in particular of the Passerines, seems to prove that in normal cases both male and female take charge of the raising of their offspring. As a rule both follow the same innate behaviour patterns, as for instance with regard to the building of the nest, the incubating, the feeding etc. It seems to be the same case with some primitive representatives of the Bowerbirds. Thus both males and females of the Aeluroedus species seem to partake of the breeding cycle. No display bower is built in such a case. Both sexes are of the same colour. Their plumage looks rather plain. As Söderberg (1929) shows very plausibly the bower may be regarded as derived from a nest. Thus the building of the bower is homologous with the building of the nest. In this connection it may be of interest that with some other kinds of Passerine birds, which no longer form a couple, the nestbuilding instinct of the male has been specially developed. In all these cases, indeed, the nestbuilding instinct serves for courting and for building a nest for the raising of the young (Penduline Titmouse, Weaver Birds, Wren etc.). Bearing this in mind, the fact that during courting the male offers leaves to the female, gets quite a different meaning. As we know the nest has been lined with leaves. It is possible that in the beginning the male only saw to the substructure of the nest, whereas he just handed the material for the inner padding over to the care of his mate, who then did the lining. In other words certain display movements as well as the construction of the bower would have to be considered as derived from the nestbuilding instinct. The preference for blue would then have to be considered as a subsequent acquisition which, perhaps, has something to do with the blue plumage of the male. The colour may have a stimulating effect on the female. In consideration of the fact that both sexes do not live together with one another the impulse to display must be intensified in order to insure the unanimity of their physiological conditions.

This theory has not been proved sufficiently so far. Anyhow it is well worth mentioning as it draws our attention to the importance of the Aeluroedus species. Only by means of a careful analysis and a comparison of the behaviour of the whole group of the Bowerbirds can the problem be solved.

The coloured film may give you some idea of the display of the Satin Bowerbird. The male is courting to a stuffed female which was kindly lent by the American Museum of Natural History. The film and the record were given to us by the New York Zoological Society, to whom we are very much indebted.

## Reference

Söderberg, R., 1929. The Genesis of the Decorative and Building Instincts of Bowerbirds. Verhdl. VI. Orn. Kongr. Kopenhagen 1926: 297–337. Berlin.

# Colourfilms: The Greeting Ceremony of the Shoe-Billed Heron, Balaeniceps rex J. Gd. and the Courtship Display of the Condor, Vultur gryphus L.

*Holger Poulsen*

*Zoological Gardens, Copenhagen*

The Shoe-Billed Heron in the Copenhagen Zoo shows a greeting ceremony towards its keeper all the year round. This behaviour is also known from other zoos e.g. Basle and Berlin. The greeting movement is a stereotype instinctive activity consisting of repeated bowing of the head and simultaneous sideway shaking of the head and when released some times (up till 40–50 times) showing central nervous fatigue and can then only be released again until some minutes later. The bird knows its keeper especially by his voice and greets him, when he enters its cage. Bowing of the head of the keeper has a strong releasing value. When a person unknown to the bird enter the cage, it is showing its intimidating display with more or less spread wings, open bill emitting hoarse notes. When excited both in intimidating display and after greeting it is sometimes clattering its bill. Probably the greeting movement is an symbolic action, because it is much alike the regurgitating of the herons when feeding their young, just as symbolic feeding in other birds. The greeting movement of the Shoe-Billed Heron is not homologous to the greeting movement of the Night-Heron, *Nycticorax nycticorax* (L.) described by Lorenz and that of the Common Heron, *Ardea cinerea* L. described by Verwey.

The Copenhagen Zoo possess a pair of Condors. In intimidation display both male and female raise themselves with somewat opened and raised wings, opened bill uttering a hissing sound. In courtship display the male with spread wings raises himself in an almost vertical line with curved and slightly swollen neck so that the lower bill almost touches the chest. Moving the tongue up and down he emits tok, tok, tok, etc. at a quick rate simultaneously slowly turning round with extended wings showing its white wing-marks. The naked reddish-grey skin of the head and the neck somewhat distended turn into a bright yellow. The display ends in a snorting sigh. Similar observations have been made by Portielje (1949).

## References

LORENZ, K., 1938. A contribution to the comparative sociology of colonial-nesting birds. Proc. 8th Int. orn. Congr. Oxford, 1934: 207–218. Oxford.

VERWEY, J., 1930. Die Paarungsbiologie des Fischreihers. Zool. Jahrb. Abt. allg. Zool. und Physiol. der Tiere. 48, 1–120.

PORTIELJE, A. F. J., 1949. Premarital behaviour in the Condor, *Sarcoramphus gryphus* L. Bijdr. Dierkunde 28, 359—371.

# Tierpsychologische Beobachtungen bei der Photographie freilebender Vögel

*Fritz Steiniger*

*Flensburg*

Die Photographie freilebender Tiere ist, wenn man von ihrer technisch-photographischen Seite absieht, ein Tätigkeitsfeld, das man recht gut als „angewandte Tierpsychologie“ bezeichnen könnte. Die Aufgabe, Abbildungen der einzelnen Vogelarten zu liefern, hat die Tierphotographie bereits weitestgehend erfüllt, so dass ihr jetzt mehr die Aufgabe zu stellen ist, Bildmaterial für die Verhaltensforschung an Vögeln zu liefern. Die dabei notwendigen tierpsychologischen Studien werden im Gegensatz zur ausgesprochen wissenschaftlichen tierpsychologischen Forschung sich meistens nicht auf eine einzelne Art beschränken, sondern werden mehr in die Breite gehen und sich gleichzeitig auf eine Reihe von Arten beziehen, die gerade Möglichkeiten dazu bieten. Man kann vielleicht erwarten, dass eine solche vergleichende und mehr in die Breite gehende Beobachtung wichtige Ergänzungen zu der mehr experimentellen Forschung an einzelnen Arten zu geben vermag.

Viele Methoden der Tierphotographie gehen von tierpsychologischen Erkenntnissen aus. Hediger hat darauf hingewiesen, dass freilebende Tiere gegenüber dem Menschen einen bestimmten Fluchtabstand einhalten, der zwar bei den verschiedenen Arten sehr unterschiedlich ist, bei den einzelnen Arten jedoch mit grosser Regelmässigkeit in der gleichen Weise festzustellen ist, wenn auch gewisse Abänderungen möglich sind, die z. B. durch Besonderheiten der Brut oder des Nahrungsmangels usw. bedingt sein können. Da dieser Fluchtabstand in der Mehrzahl der Fälle zu gross ist, um selbst unter Verwendung eines Tele-Objektivs schon brauchbare Aufnahmen zu gestatten, so ist die Hauptfrage der Tierphotographie: Wie kann man diesen als durchschnittlich aufzufassenden Fluchtabstand um ein Wesentliches unterschreiten, ohne die Fluchtreaktion auszulösen? Im Sinne der Umweltlehre von Uexkülls ist der Mensch gewöhnlich bei stärkerer Annäherung in den „Feindeskreis“ eines freilebenden Vogels oder

Säugetieres „eingeklinkt". Es fragt sich: Ist es möglich, ihn aus diesem Feindeskreis auszuklinken?

Wir wissen aus zahlreichen Untersuchungen von verschiedenster Seite, dass bei vielen Vögeln ein angeborenes oder erworbenes Bild z. B. von Raubvögeln oder anderen Feinden besteht, das ziemlich merkmalsarm ist. Denn z. B. das Vorführen von Atrappen des Raubvogels, die nur noch die Silhouette wiedergeben und auch diese noch in abgewandelter Form, wird mit Flucht- oder Drückreaktion beantwortet. Wir dürfen aus bisherigen Beobachtungen folgern, dass auch das Bild des Menschen für einen Vogel merkmalsärmer ist als in den Augen eines Menschen selbst. Ja, wir wissen nicht einmal, ob in zahlreichen oder weniger zahlreichen Fällen überhaupt ein für den Menschen spezifisches Bild vorhanden ist, und ob dieses Bild nicht zugleich noch eine Zahl von Tierarten mit vorwiegender Feindtönung umfasst. Beim Jungvogel scheint ein Bild des Menschen oft weitgehend zu fehlen. Es wird durch Auslöser ersetzt, die im Verhalten der Altvögel gegeben sind, z. B. durch Warnrufe. Fehlen die Warnrufe oder bei Nestflüchtern das Fluchtvorbild der Altvögel, so erhält der Mensch in der Umwelt des Jungvogels oft keine Feindtönung, er gerät z. B. in das Bild des Elternkumpans hinein und wird angesperrt. Ein junger Star (*Sturnus v. vulgaris* L.) lässt sich am ersten Flugtage bei einiger Vorsicht noch mit dem Finger berühren (Fig. 1). Er richtet sich noch ganz nach dem Verhalten, insbesondere nach den Warnrufen der Altvögel. Dies gilt für sehr viele junge Vögel. Wenige Tage später ist jedoch das der Art eigentümliche Fluchtverhalten schon ziemlich vollständig entwickelt.

Eine Komponente des Fluchtverhaltens gegenüber dem Menschen ist dabei sicher angeboren, das ist die Fluchtreaktion auf schnelle oder mittelschnelle Bewegung eines grösseren Körpers in geringer Entfernung. Auch soeben ausgeflogene Jungvögel pflegen sofort die Flucht zu ergreifen, wenn man in ihrer Nähe eine hastige Bewegung ausführt. Es kommt daher bei der Photographie freilebender Vögel ganz besonders darauf an, jede hastige Bewegung zu vermeiden, jeden Griff und jede Wendung zeitlupenhaft langsam auszuführen.

Während schnelle Bewegungen, die auch die vertrautesten Stubenvögel und Haustiere stets sofort zu einer schnellen Fluchtreaktion veranlassen, wohl bei jeder Vogelart den Menschen wenigstens vorübergehend in ein Feindschema einklinken, sofern er nicht zu weit entfernt ist, scheint es sonst jedoch einige Arten zu geben, bei denen überhaupt eine Fluchtbeziehung zum Menschen gar nicht besteht, die man irgendwie als spezifisch bezeichnen könnte. Es sei auf die im Herbst und Winter nach Mitteleuropa kommenden Seidenschwänze (*Bombycilla g. garrulus* L.) hin-

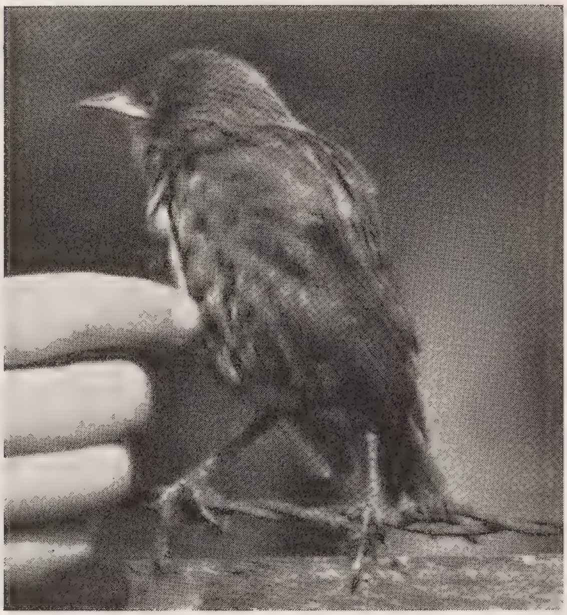


Fig. 1. Junger Star kurz nach dem Ausfliegen, lässt sich mit der Hand berühren.

gewiesen, die man manchmal fast mit der Hand berühren kann, ohne dass sie fortfliegen. Auch die Wassertreter (*Phalaropus fulicarius* und *lobatus* L.), die auf dem Herbstzuge an die Nord- und Ostseeküste kommen und meistens flache, nicht salzhaltige Gewässer in der Nähe der Küste aufsuchen, beachten die Gegenwart eines Menschen in ihrer Nähe so gut wie gar nicht. Man kann auf 1 m und weniger an die Vögel herankommen, und ein Mitarbeiter der Vogelwarte Rossitten berichtete darüber, dass ein Wassertreter dem Beobachter sogar zwischen den Beinen hindurchgeschwommen sei. Ebeñso ist es manchmal bei aus dem Norden kommenden Raubmöwen (*Stercorarius* sp.), wie van Oordt aus Holland berichtet. Hediger bezeichnet dieses Verhalten dem Menschen gegenüber, das man bei Tieren, die aus menschenleeren Gegenden kommen, beobachten kann, als Pseudozahmheit.

Der Mensch nimmt in diesem Zusammenhang keineswegs eine Sonderstellung ein. Auch bestimmten, gewöhnlich nicht als Verfolger auftretenden Tierarten gegenüber vermisst man bei Vögeln manchmal die Fluchtbeziehung. Es war für mich sehr überraschend zu beobachten, dass bei einem sehr starken Rattenbefall der Vogelinsel Norderoog an der Schleswig-Holsteinischen Westküste bogenschnäblige Strandläufer (*Calidris*

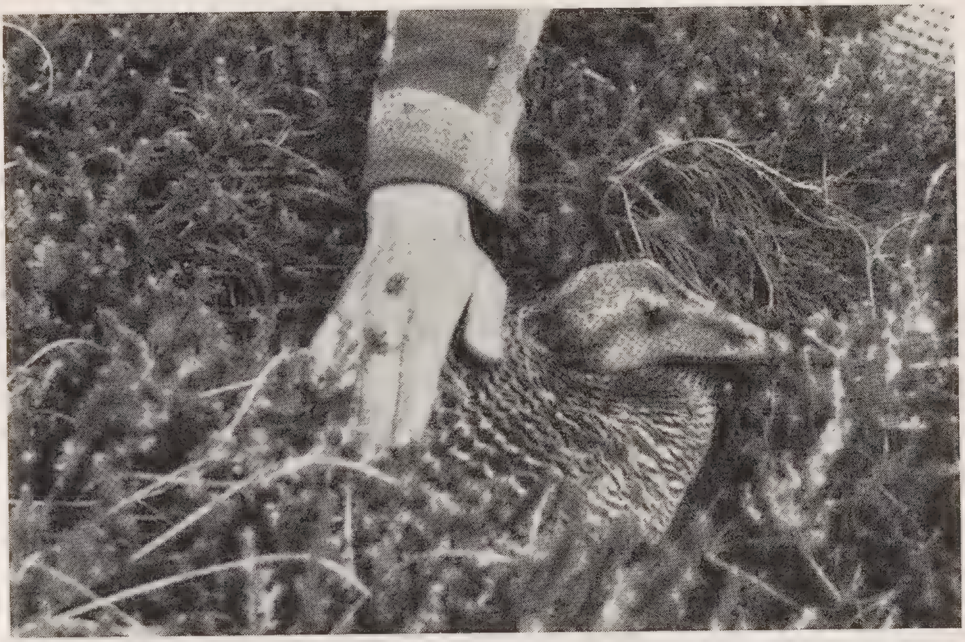


Fig. 2. Brütende Eiderente, lässt sich mit der Hand berühren.

*ferruginea* Pontoppidan) und Kanutstrandläufer (*Calidris c. canutus* L.) den umherlaufenden Ratten gegenüber kaum einen Fluchtabstand einhielten und von den Ratten ziemlich mühelos erbeutet wurden. Andere Arten, wie Rotschenkel (*Tringa t. totanus* L.) und Austernfischer (*Haematopus o. ostralegus* L.), die an der deutschen Nordseeküste zahlreich brüten, hielten den Ratten gegenüber meistens einen Fluchtabstand von einigen Metern ein. Sie warnten sogar, wenn sie die Ratten erblickten, und fielen ihnen meistens nur dann zum Opfer, wenn die Ratten sie auf unübersichtlichem Gelände aus der Deckung heraus ansprangen.

Ohne diese Beobachtung verallgemeinern zu wollen, würde man hier von einer Pseudozahmheit im Sinne Hedigers den Ratten gegenüber sprechen können.

Auch der Bruttrieb kann, wie allgemein bekannt, den Fluchtabstand ganz wesentlich herabsetzen oder ihn völlig aufheben. Eine brütende Eiderente (*Somateria mollissima* L.) kann man manchmal auf dem Nest mit der Hand berühren (Fig. 2). Beim Sandregenpfeifer (*Charadrius hiaticula* L.) kommt man in den letzten Tagen der Brut, wenn man nicht plötzlich an das Gelege herantritt sondern den Vogel erst einige Zeit an die Gegenwart des Menschen gewöhnt und vorsichtig auf dem Boden herankriecht, sehr

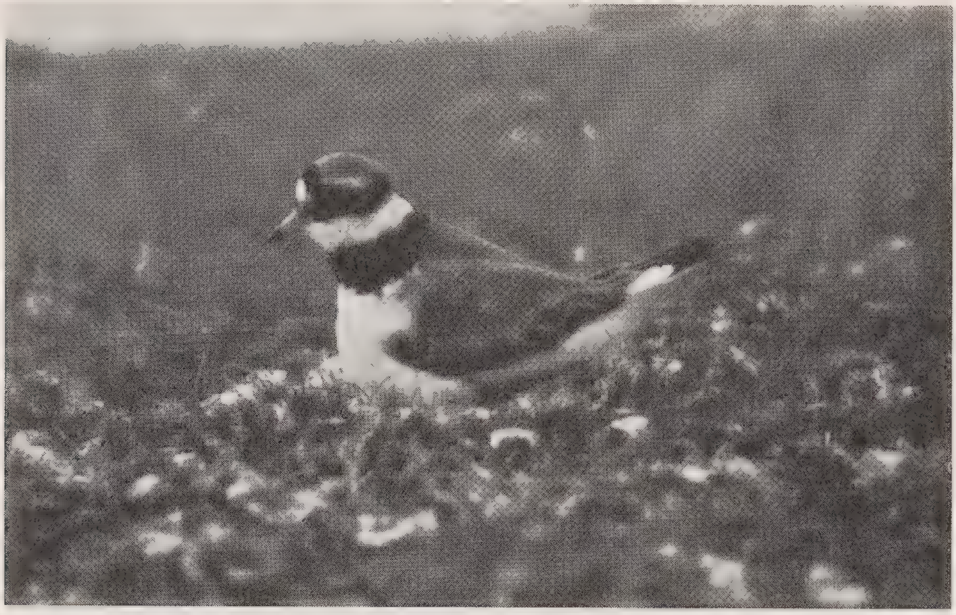


Fig. 3. Aufs Nest gehender Halsbandregenpfeifer, 1 m vor dem Photographen.

häufig bis auf Entfernungen von weniger als 1 Meter heran (Fig. 3). Und es sei auch an den Mornellregenpfeifer (*Charadrius morinellus* L.) von Bengt Berg erinnert, der sogar noch aufs Gelege ging, wenn die Eier in der Hand des Menschen lagen. Eine ganze Reihe ähnlicher Beobachtungen sind im amerikanischen Schrifttum veröffentlicht. Man hat diese durch den immer stärker werdenden Bruttrieb bedingten Besonderheiten des Verhaltens viel für Aufnahmen benutzt, die dann auch mit ganz kurzbrennweitigen Apparaten möglich waren.

Bei Aufnahmen am Nest pflegt man sonst nach der seit 50 Jahren üblichen tierphotographischen Anfängermethode Schirme in Zeltform zu verwenden, in denen man wartet, bis der brütende Vogel wieder aufs Nest geht. Diese Methode ist zwar nicht sehr sportlich, aber in manchen Fällen nicht zu umgehen. Gewöhnlich hält die Fluchtreaktion auf den ins Versteck gegangenen Menschen nur sehr kurze Zeit an. Ist er nicht mehr zu sehen und macht er sich nicht durch Bewegungen bemerkbar, so geht der Vogel nach 1/4 bis 1/2 Stunde wieder aufs Nest. Diese Zeit lässt sich im Durchschnitt in einer sehr auffallenden Weise dadurch verkürzen, dass der Photograph einen Begleiter zum Zelt mitnimmt, der nach Beziehen des Verstecks sich wieder entfernt. Damit wird ein normaler Vorgang in der Umgebung des

Brutvogels vorgetäuscht, nämlich Annäherung eines Wesens mit Feindtönung und anschliessend sein Fortgehen aus der Nähe des Nestes, so dass der Vogel etwa ebenso schnell wieder aufs Gelege geht, wie er dies gewöhnlich tut, wenn er einmal vorübergehend beim Brüten aufgescheucht wird. Auch spielt es eine grosse Rolle, wenn das Versteck schon einige Tage irgendwo in der weiteren Umgebung des Nestes gestanden hat und den Vögeln bekannt ist. Auf seine Ortsveränderung beim Heranstellen an das Nest reagieren die Vögel dann gewöhnlich viel weniger, als wenn hier plötzlich ein ganz neuer und ungewöhnlicher Gegenstand zu sehen ist.

Es ist nicht gerade überraschend, wenn man häufig beobachtet, dass nach Aufstellen und Beziehen des Verstecks immer nur einer der Partner des betreffenden Brutpaares zum Nest kommt, während der andere keinerlei Anstalten macht, die entblössten Eier zu bedecken, auch wenn der andere Partner dies nicht tut. Die erfolgte Brutübergabe, die bei vielen Arten mit besonderen, manchmal recht artspezifischen Zeremonien verbunden ist, scheint dabei für die Verpflichtung zum Brüten verbindlich zu sein. Der Partner, der das Brüten abgegeben hat, unternimmt meistens keinerlei Versuche, auf das Gelege zu gehen, bis er wieder durch die Brutübergabe das Brutgeschäft übernimmt. Diese Beziehung scheint durch das erschwerende Moment des in Nähe des Geleges aufgestellten Verstecks noch gefestigt zu werden, wenn auch Ausnahmen immerhin vorkommen, z. B. bei stark erhöhtem Bruttrieb kurz vor dem Schlüpfen der Jungen. Allerdings kommt es vor, dass sie kurz nach erfolgter Brutübernahme noch rückgängig gemacht wird, wenn der die Brut übernehmende Partner vorher noch nicht in Nähe des aufgestellten Verstecks gebrütet hat. Z. B. beobachtete ich von einem 3 m neben dem Gelege eines Zwergseeschwalbenpaares (*Sterna a. albifrons* Pal.) aufgebauten Zelt aus folgendes: Der vor Aufstellen des Zeltes brütende Vogel kam sehr schnell wieder auf das Gelege. Nach etwa einer Stunde erfolgte die Brutübergabe mit einem Zeremoniell, bei dem beide Partner mit erhobenem Schwanz und schräggestellter Körperlängsachse vor den Eiern standen und dabei erregt riefen. Der neu hinzukommende Partner war durch eine Anomalie der Kopfplattenzeichnung kenntlich und zeigte bei der Paarung männliches Verhalten. Nachdem dieser Vogel nicht mehr von der Übergabezeremonie und dem Bedecken der Eier in Anspruch genommen wurde und seine Umgebung aufmerksamer beobachtete, flog er mit einem Schrecklaut auf, man könnte vermenschlichend sagen, weil ihm die Situation mit dem daneben stehenden Zelt als zu gefährlich erschien. Darauf hin kehrte der andere Partner wieder auf das Gelege zurück und brütete weiter. Dieser Vorgang wiederholte sich in 10 Minuten in ganz der gleichen Form, dann noch weiterhin insgesamt achtmal in den beiden nächsten Stunden, bis der gekennzeichnete Partner endlich auf dem Gelege sitzen blieb. Eine fast in allen Einzelheiten übereinstimmende Beobachtung machte ich am Nest eines Uferschnepfenpaares (*Limosa limosa* L.), bei dem der eine Vogel rostrot, der andere fahlbraun gefärbt war. Ich konnte ähnliche Situationen auch künstlich bei Küstenseeschwalben (*Sterna macrura* Naum.) und Trauerseeschwalben (*Clidonias n. nigra* L.) auslösen, wenn ich den das Brutgeschäft übernehmenden Partner kurz nach der Ablösung durch einen schnellen Stoss gegen die Zeltwand aufschreckte. Längere Zeit nach der Brutübergabe dagegen scheint für den abgelösten Partner meistens eine Brutverpflichtung nicht mehr zu bestehen, wenn es sich nicht gerade um die Zeit stärksten Bruttriebes in den letzten Tagen vor dem Schlüpfen der Jungen handelt.

Die ungewöhnliche Erschwerung des Aufsnestgehens durch das in Nestnähe aufgestellte Versteck lässt manchmal auch ein Verhalten sichtbar werden, das man gewöhnlich nicht sieht, nämlich ein ,,Zum-Neste-Treiben'' des zum Brüten verpflichteten Partners durch den brutdienstfreien Partner. Wiederholte und eindeutige Angriffe des brutdienstfreien Partners auf den zur Brut verpflichteten sah ich bei Lachmöwe, Trauerseeschwalbe, Kiebitz, Seeregenpfeifer, Austernfischer und andeutungsweise beim Rotschenkel. Bei einem eine Reihe von Tagen im Beginn der Brut beobachteten Kiebitzpaar, bei dem ich Männchen und Weibchen gut unterscheiden konnte, nahmen die Angriffe des Männchens auf das zögernde Weibchen sogar sehr derbe Formen an. Das Weibchen wurde auf die Seite geworfen, aus der Luft angeflogen und umgerempelt und auch mit Schnabelhieben bedacht, bis es sich zum Weiterbrüten entschloss. Jedes Mal, wenn es vom Nest aufstand, wurde es sofort in der gleichen Weise vom Männchen angegriffen, so dass der Zusammenhang ganz eindeutig war. Es wagte sich schliesslich überhaupt nicht mehr vom Nest herunter, anscheinend wurde die Furcht vor den rasenden Angriffen des Männchens grösser als die vor dem im Zelt versteckten Menschen, und als ich schliesslich aus dem Zelt herauskam, um den Ansitz abzubrechen, blieb das Weibchen trotzdem in einer an das bekannte ,,Sich-Lahmstellen" erinnernden Haltung auf den Eiern liegen, so dass ich noch mehrere Aufnahmen von ihm machen konnte (Fig. 4). Das Männchen kam während der ganzen Zeit niemals an das Versteck bis auf Aufnahme-Entfernung heran, sondern griff das Weibchen erst an, wenn es 15 bis 20 m vom Nest fortgelaufen war.

Beim Kiebitz und beim Seeregenpfeifer war der zum Nest treibende Partner mit Sicherheit das Männchen, beim Austernfischer mit allergrösster Wahrscheinlichkeit, und auch bei Lachmöwe, Trauerseeschwalbe und Rotschenkel sprach vieles für den gleichen Zusammenhang, obwohl man bei

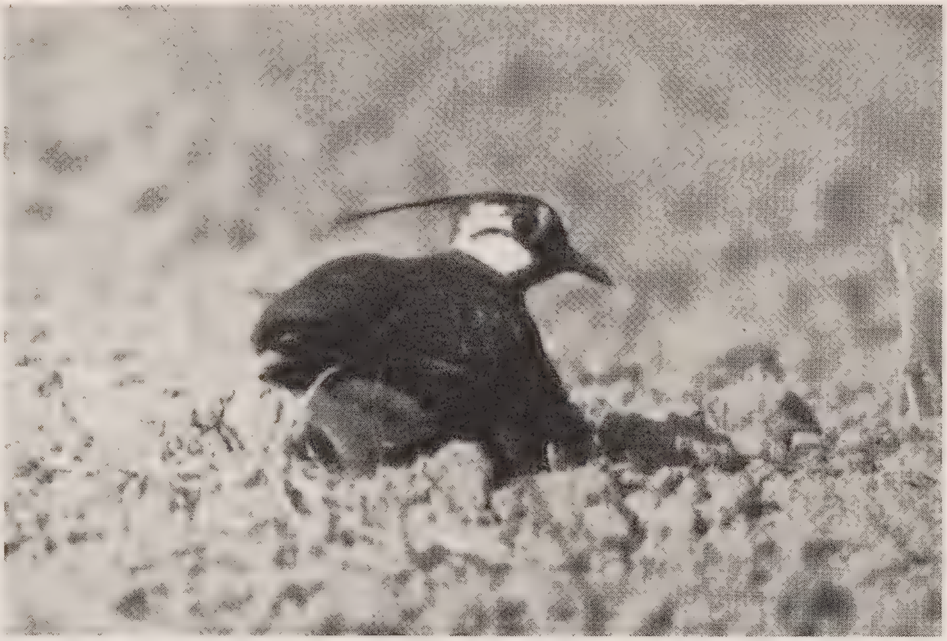


Fig. 4. Beim Brüten aufgeschreckter Kiebitz, der ein an das „Sich-Lahmstellen“ erinnerndes Verhalten zeigt.

diesen Arten nur dann einen sicheren Schluss auf die Geschlechtszugehörigkeit eines Tieres ziehen kann, wenn man die Eiablage gesehen oder den Vogel durch Sektion untersucht hat. Jedenfalls war es immer nur einer der Partner, der sich dabei stets aktiv, und der andere, der sich stets passiv verhielt. Bei einem Seeregenpfeiferpaar sah ich zwar, wie das leicht am Gefieder zu erkennende Männchen das Weibchen bedrohte, wenn dieses während seiner Brütezeit das Gelege verliess; als jedoch das Männchen nach einiger Zeit das Weibchen ablöste und nun seinerseits einige Male durch Windbewegungen einer Zeltwand vom Gelege vertrieben wurde, so lief das Weibchen zwar unter Warnrufen um das Männchen herum, machte jedoch keine Angriffe oder Scheinangriffe. Ich möchte diese Beobachtung im Zusammenhang mit einer kürzlich erschienenen Arbeit von Frau Nice hervorheben, in der sie darauf hinweist, dass ein Inferiorismus des Weibchens bei Vögeln eigentlich nicht bestehe. Doch glaube ich, dass die Beobachtungen über das Zum-Neste-Treiben durch das Männchen wohl mehr für als gegen das Bestehen einer derartigen Beziehung sprechen.

Wenn ich den Ansitz an einem Nest beendete, so führte ich gewöhnlich Versuche zu der Frage durch, welche optischen Auslöser der Mensch dem

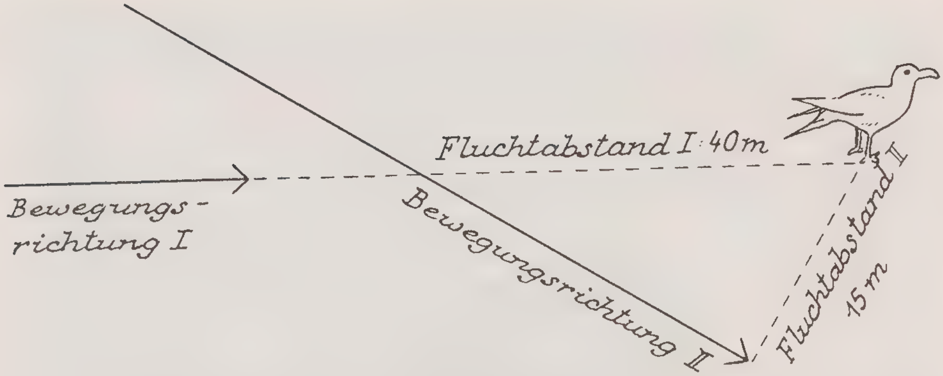


Fig. 5. Verschiedenheit des Fluchtabstandes bei direkter Annäherung (Bewegungsrichtung I, 40 m) und bei seitwärts vorbeiführender Bewegung (Bewegungsrichtung II, 15 m).

Vogel bieten muss, damit er Feindtönung erhält und die Flucht veranlasst. Ich öffnete dazu mit ganz langsamen Bewegungen (zeitlupenartig) das Zelt und liess mich nach und nach für den Vogel sichtbar werden. Die bekleideten Füsse oder sonstige bekleidete Körperteile lösten die Flucht nicht aus. Auch wenn ich bei grosser Hitze im Sommer im Badeanzug im Zelt sass, so war der gebotene Anblick der glatten Haut, z. B. der Brust oder des Oberschenkels, für den Vogel meistens noch nicht alarmierend. Dagegen lösten unbekleidete Finger und Zehen sofort die Flucht aus. Noch viel heftiger erfolgte die Flucht bei Anblick des Auges, während andere Partien des Gesichts, z. B. Nase und Mund, wenig wirkten. Auch bei freisitzenden Vögeln, denen ich mich ohne Versteck näherte, beobachtete ich sehr regelmässig, dass sie schleunigst die Flucht ergriffen, wenn ich sie direkt ansah. Näherte ich mich jedoch in der Weise, dass ich auf kürzere Entfernung den Kopf nach unten beugte und den Vogel nur auf der Mattscheibe des Photoapparates betrachtete, so kam ich meistens näher an ihn heran. Es ist ja eine ganz bekannte Tatsache, dass auf den Bäumen am Rande einer viel begangenen Strasse sitzende Krähen nicht auffliegen, wenn man unter ihnen vorbeigeht, dass sie dies jedoch sofort tun, wenn man einmal nach oben blickt. Das auf den Vogel gerichtete Auge scheint also in ganz besonderem Masse ein Auslöser für die Fluchtreaktion zu sein.

Auch die Bewegungsrichtung des Menschen ist für das Auslösen der Flucht eines Vogels von Bedeutung. Die direkte Richtung auf einen Vogel zu lässt diesen in sehr viel grösserem Abstand flüchtig werden, als wenn die Bewegung seitlich an ihm vorbeiführt. Z. B. bei einer Raubmöwe auf dem völlig freien Watt an der Westküste Schleswig-Holsteins, die nicht sehr scheu war, kam ich bei Annäherung in direkter Richtung auf 40 m heran, bei Annäherung in seitlicher Richtung jedoch auf 15 m (Fig. 5). Die Möwe flog immer nur ganz kurze Strecken weiter, so dass ich beide Versuche mehrmals wiederholen konnte. Diese Beobachtung erscheint als trivial, wenn wir sie ins Menschliche übertragen. Auch wir würden vor einem in seiner Haltung uns gegenüber fraglichen Wesen, z. B. vor einem Stier auf freiem Felde, viel schneller die Flucht ergreifen, wenn er direkt auf uns zu kommt, als wenn er seitwärts an uns vorbeiläuft.

Wenn man an frei am Strande stehende Strandläufer herankommen will, so ist es sehr auffallend, dass bei aufrechtem Gang der Fluchtabstand der Vögel etwa dreimal so gross ist, wie wenn man mit langsamen Bewegungen und möglichst flach auf dem Boden auf allen Vieren an sie herankriecht. Bei bogenschnäbligen Strandläufern (*Calidris ferruginea*) gelang es mir gar nicht selten, bis auf 2 m heranzukommen, ebenso bei Sanderlingen (*Crocethia alba* Pal.). Manchmal befand ich mich dabei mitten in einer ganzen Schar, während es sonst im allgemeinen viel schwerer ist, an eine Vogelschar heranzukommen als an einen Einzelvogel, weil in einem grösseren Verbande von Tieren immer einige zu sein pflegen, die früher abfliegen und dann bei der Flucht die anderen mit sich reissen. Auf flachem Boot liegend kann man sich mit dem Wind viel näher an Strand- und Schwimmvögel herantreiben lassen als etwa bei Annäherung in aufrechtem Gang.

Der sich flach am Boden weiterbewegende Mensch scheint einen oder einige Auslöser für die Fluchtreaktion nicht zu haben, die beim aufrecht gehenden Menschen bestehen. Möglicherweise bekommt der flach am Boden sich bewegende Mensch in der Umwelt des Vogels die gleiche Bedeutung wie eine Robbe oder ein anderes für die Vögel harmloses Tier, so dass sehr viel weitergehend das Fluchtmotiv fortfällt.

Der Fluchtabstand im Sinne von Hediger ist also nichts absolut Gegebenes sondern lässt Abwandlungen entsprechend der jeweiligen Situation zu, in der sich der Vogel als Subjekt gerade befindet. Die ,,Tönung“ des Menschen als ,,Feind“ in der Umwelt des Vogels zeigt offensichtlich starke graduelle Verschiedenheiten. Diese können nicht nur quantitativer sondern auch qualitativer Natur sein. In den von Gewässern durchzogenen Grünanlagen von Berlin (und auch von anderen Grosstädten) hielten sich vor dem Kriege in den Wintermonaten zahlreiche Stockenten auf, die von den Besuchern der Anlagen regelmässig gefüttert wurden und das Dargebotene oft aus der Hand abnahmen. Es handelte sich dabei um ein ortsgebundenes Verhalten, das wahrscheinlich durch das Beispiel von freifliegenden Zootieren entstanden war, und das es ermöglichte, den Menschen örtlich ganz aus dem Feindeskreis der Enten auszuklinken. Dabei handelte es sich nicht etwa um freifliegende Zootiere sondern um wilde Stockenten, die im Winter scharenweise in die Grosstädte kommen. Die Gewohnheit, sich dem Menschen bis auf wenige Meter oder gar bis zur Abnahme von Futter aus der Hand zu nähern, blieb jedoch streng ortsgebunden. Es war für mich überraschend, festzustellen, dass eine aus etwa 30 Tieren bestehende Stockentenschar, die sich an der Potsdamer Spreebrücke aus 2—5 m Entfernung von tierfreundlichen Leuten füttern liess, einen Fluchtabstand von mindestens 30 m einhielt, wenn sie etwa 600 m weiter zum gegenüberliegenden Ufer des vor der Brücke gelegenen kleinen Sees geflogen war. Ich habe diese Stockentenschar im Februar 1939 zwei Tage lang beobachtet und die verschiedensten Annäherungsversuche gemacht. Es blieb immer so: Die Enten liessen sich an der Brücke füttern, waren jedoch schon in kurzer Entfernung von dieser recht scheu.

Diese wenigen hier beliebig ausgewählten Beobachtungen aus einer 25-jährigen tierphotographischen Tätigkeit mögen zeigen, dass der Fluchtabstand eines Vogels, mit dem sich der Tierphotograph auseinanderzusetzen hat, weit stärker wandelbar ist, als es bei der Einführung dieses Begriffes durch Hediger zum Ausdruck kommt.

# Population Ecology in Birds
## A Review

*David Lack*

*Edward Grey Institute of Field Ornithology, Oxford*

### Introduction

Population ecology is the newest of the four subjects reviewed at this Congress, indeed the present seems the first synthesis of it that has been attempted for birds. The fundamental concepts of the subject have been formulated primarily in connection with other branches of zoology, first in mathematical terms by Lotka (1925) and Volterra (1928, 1931), and later in logical terms by the entomologists A. J. Nicholson (1933) and H. S. Smith (1935), while to another entomologist, Varley (1947), is due the first intensive attempt to apply these theoretical ideas on a quantitative basis to a wild population. As they have not been concerned specifically with birds, these important theoretical studies will not be discussed further here. Moreover, as time is limited, I will be citing only a selection from the work on bird populations. This review is an attempt at a synthesis of ideas, not a comprehensive summary of work done. It falls readily into two sections, first a consideration of censuses and other over-all studies of population fluctuations, and secondly a consideration of the factors involved in population increase and decrease.

### Part I. Population Changes

#### *Census work*

Bird populations are capable of an exceedingly rapid increase, though this is rarely found in nature except where a species has colonised a new area, or when it is recovering after some abnormal disaster. The best recorded example is that shown in Fig. 1. When 8 Pheasants (*Phasianus colchicus*) were introduced to an island off the coast of Washington previously inaccessible to them, the birds increased in only five years to a breeding population of 1325 (Einarsen 1945). Most unfortunately, the experiment was then interrupted by the war. It is to be hoped that comparable experiments may be made elsewhere.

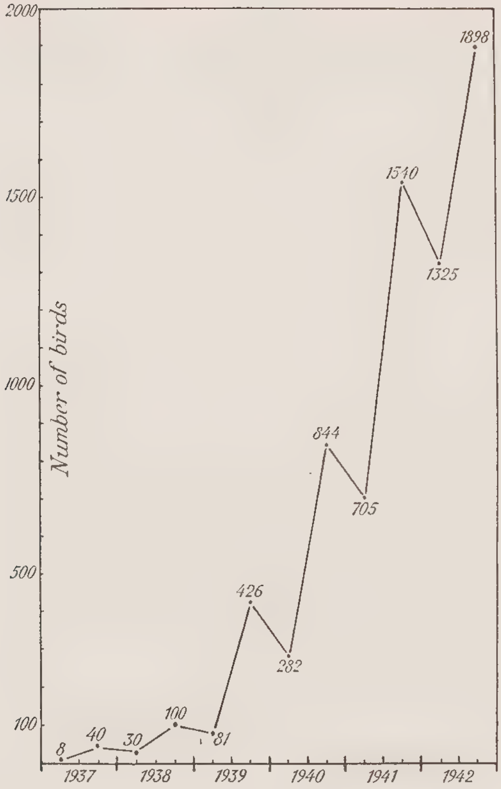


Fig. 1. Increase of *Phasianus colchicus* on Protection Island, Washington. (Census each spring and fall) (after Einarsen).

More usually, a bird population remains fairly stable, as shown in Fig. 2 for the Heron (*Ardea cinerea*) in England, where a sample census has been carried out by the British Trust for Ornithology for twenty years (Nicholson, E. M. 1935–38; Alexander, 1940–50). The Heron population decreases markedly whenever there is a hard winter, but then recovers rapidly until it reaches its previous high density, after which there is no further increase. This implies that a stringent control is operating when the density is at its usual high level, but that, when the density is well below this level, the control is relaxed. In other words, the control is density-dependent. There is no reason to think that the reproductive rate (i. e. the clutch-size) of the Heron varies appreciably with density, and the regulation in question is presumably due to a rise in the mortality-rate when the density is high.

The operation of density-dependent mortality can be seen more clearly in some of Errington's data on the Bobwhite Quail (*Colinus virginianus*).

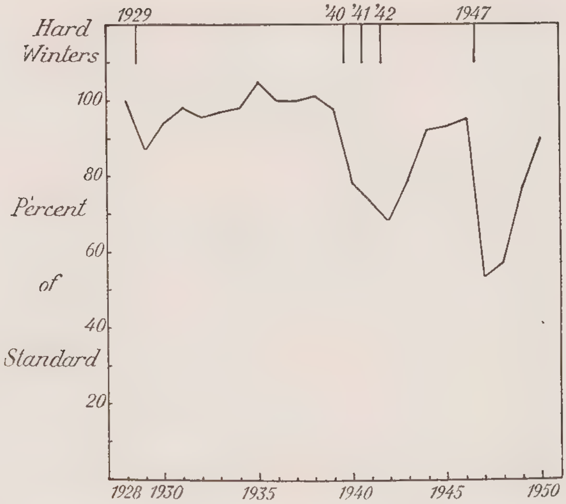


Fig. 2. Sample Census of *Ardea cinerea* in Britain (after Nicholson and Alexander).

Errington (1945) censused a Bobwhite population twice each year, in April and November. This enables the population changes in summer and winter to be analysed separately, and my re-analysis of his summer data is set out in Fig. 3. In Fig. 3A the approximate density of the Bobwhite in summer, just after breeding, is plotted against the density in the following November of each year. The density in November does not bear a fixed relation to that of the previous summer; instead, when the summer density is higher, there is a greater falling away before November. In Fig. 3B, where the summer density in each year is plotted against the percentage reduction (mortality) by November, it can be seen that proportionate mortality rises as density rises.[1]

---

[1] Errington himself plotted the April density against November density in terms of proportionate *increase*. This is misleading, because what has really happened between April and November is first an *increase* due to breeding, followed by a *decrease* from midsummer to November. As clutch-size is not known to vary with population density, it is almost certainly not the increase before midsummer but the decrease thereafter which is density-dependent. Unfortunately, the density just after breeding was recorded in only one year, when it was 4.1 times the April density. This factor will not, of course, have been the same each year, but as there is no reason to think that it varied with population density, it seems best to multiply the April density by a constant (4.1) in order to assess the relation of the autumn decrease to density. Hence the figures for summer density in Fig. 3 are my calculated, not Errington's observed, values, but the resulting graph is, I consider, nearer to reality than is Errington's plot in terms of November *increase*. Actually, since all that I have done is to multiply Errington's April figures by a constant, my graph looks very similar to his.

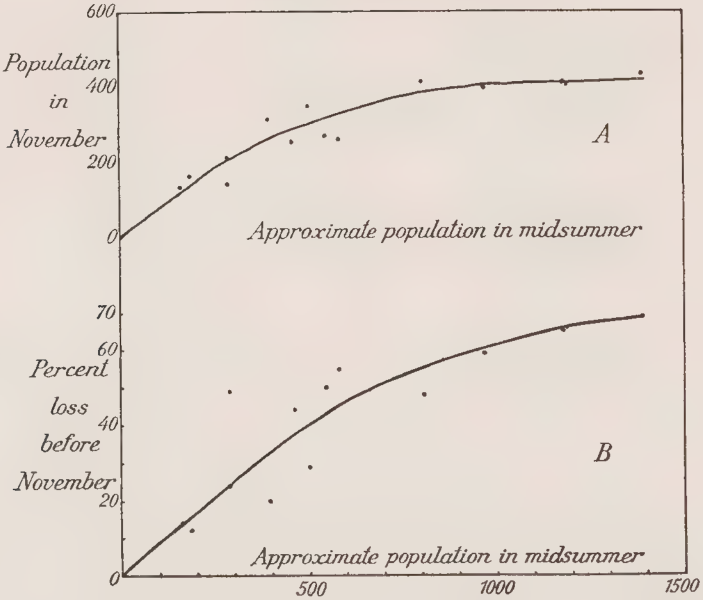


Fig. 3. Fall mortality of *Colinus virginianus* (1930–43) (after Errington).

Figs 2 and 3 illustrate a direct relation between population density and proportionate mortality; and since mortality rises as density rises, it is easy to see how the population is kept in check. There is also another, and more complex, type of relationship possible between mortality and density. If a population increases steadily in numbers for several years, and then decreases steadily for several years, the relation between proportionate mortality and density is very different. During the period of increase the mortality-rate is low, both at the initial low and the subsequent high density, while during the period of decrease the mortality-rate is high, both at high and later at low densities. Hence if the data are plotted in the manner of Fig. 3B, no relation is at first apparent between mortality and density, for low mortality-rates occur at both high and low densities, and high mortality-rates similarly. If, however, instead of trying to fit the points to a curve of the type in Fig. 3B, the points for successive years are joined in order of date, it is found that they tend to lie on a closed curve. Professor Varley has pointed out to me that Errington's figures for the winter mortality of the Bobwhite are of this type. Fig. 4A shows the steady rise and subsequent steady fall of the Bobwhite population (Errington's April census) for the first ten years of his study. Fig. 4B shows the initial population density each November plotted against the percentage loss during the ensuing win-

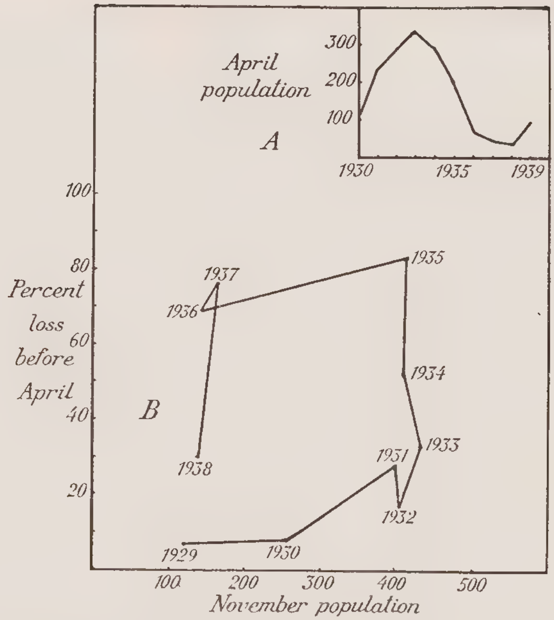


Fig. 4 A. April census of *Colinus virginianus* (1930–40) (after Errington).
B. Winter mortality of *Colinus virginianus* (1929–38) (after Errington).

ter. From his data, Errington concluded that the Bobwhite's winter mortality was not density-dependent. It is true that it was not directly density-dependent, but if the points in Fig. 4B are joined in order of date, they approximate to a closed curve.

The above situation is typical for cyclic changes in population density. In particular, it is found when population density is controlled by what Varley (1947) terms a delayed density-dependent factor. For instance, in predator-prey oscillations of the classical type, the prey density rises steadily for several generations, and then steadily falls, and the predator population shows parallel changes, but lagging behind. If prey mortality is plotted against prey density, the points for successive generations form a closed curve, ideally a circle (see for instance Gause, 1934). In such a case, the prey mortality is not directly related to the prey density, but nevertheless, it is density-dependent, for it depends on the predator density, and the latter has been determined by the prey density at an earlier stage. The effect of the prey density on mortality is therefore a delayed one.

While a cyclic rise and fall of the population involves mortality relationships of the type in Fig. 4B, and is characteristic of the influence of a delayed density-dependent mortality factor, the presence of the latter should not be assumed in any particular case without direct evidence. In fact, Errington found no correlation between the mortality of the Bobwhite and the density of its predators, and attributed most of the winter losses in question to "emergency" (i. e. density-independent) factors. Further, the apparent regular cycle did not persist beyond the first nine years of his study, and thereafter the population fluctuated erratically. The observed population changes in the Bobwhite might therefore have been due to a combination of density-independent factors which happened to result in a regular pattern over a period of nine years. The particular interest of Errington's study is that the summer and winter losses showed a quite different relationship to density. The difference between direct and delayed density-dependent factors should be kept in mind by future workers.

A twice-yearly census has also been made over twelve years for another American gallinaceous species, the Ruffed Grouse (*Bonasa umbellus*) (Bump *et al*, 1947). When I plotted the figures for summer and winter losses against density obtained in this study, I did not find relationships of the type of either Fig. 3B or Fig. 4B. Indeed, no regular relationships were apparent, suggesting that a multiplicity of factors, some of them density-independent, were involved, and no firm conclusion could be drawn. Few other long-term bird censuses are yet available for analysis. Those covering at least ten consecutive years and involving at least 50 pairs are cited in Table 1, omitting a few sea-bird censuses in which, as colonies may shift *en bloc*, a total of far more than 50 pairs is required to establish the true fluctuations. The last column in Table 1 shows those studies in which the productivity

Table 1. Long-term Censuses of Species.
(At least 10 consecutive years, at least 50 pairs.)

| Species | Years | Place | Author | Productivity also measured |
|---|---|---|---|---|
| *Ardea cinerea* ...... | 1928–50 | England | Nicholson (1935–38)<br>Alexander (1940–50) | |
| *Ciconia alba* ...... | 1928–39 | Oldenburg | Schüz (1940) after Tantzen | + |
| *Ciconia alba* ....... | 1933–42 | Insterburg | Hornberger (1943) | + |
| *Colinus virginianus* . | 1929–44 | Wisconsin | Errington (1945) | + |
| *Bonasa umbellus* .... | 1930–42 | New York | Bump *et al.* (1947) | + |
| *Sturnus vulgaris* .... | 1936–47 | N.W. Saxony | Berndt (1949) | |
| *Muscicapa hypoleuca* | 1936–47 | N.W. Saxony | Berndt (1949) | |
| *Parus major* ....... | 1912–42 | Holland | Kluijver (*in press*) | + |

(young raised or young surviving to autumn) was measured in addition to the breeding population.

When these various censuses are plotted graphically, they illustrate that:

a) bird populations show *restricted fluctuations*. The latter seems a better term than A. J. Nicholson's "balance." The point is that, compared with the increase and decrease of which they are theoretically capable, animal populations in nature show extremely small fluctuations, with a marked tendency to return to the *status quo*. But to describe this state of affairs as a "balance" is to over-stress the stability, as the presumed point of the balance is continually shifting somewhat in response to both short-term and long-term factors;

b) the fluctuations are irregular (except in a few regular cycles, to be discussed later);

c) the average interval between peak populations, and the heights of the maximum and minimum densities above the average, differ in different species of birds. In the censuses cited in Table 1, the slowest fluctuations occur in the White Stork (*Ciconia alba*) and the most rapid in the Great Tit (*Parus major*).

Without a simultaneous study of the causes of mortality, these long-term censuses tell one very little. The irregularity of the fluctuations presumably means that many factors affect the population density; hence a far longer period than ten to twenty years is needed before firm conclusions can be drawn. It should be added, also, that the mathematics of serial correlations is difficult, and that the statistical methods used for studying other types of biological variation do not necessarily apply to time series (see for instance Moran, 1949).

In studying population graphs, it should also be kept in mind that a plot of the breeding population each year gives a misleading idea of what is happening. Fig. 5, for instance, shows the population of the Great Tit (*Parus major*) in a wood near Oxford over four years (J. A. Gibb, 1950 and in progress). In this period the successive breeding populations, connected by the dotted line, show a steady increase. The real population changes were much more complicated, as shown by the intervening points on the graph, connected by a continuous line. There was each year a very rapid increase when the young left the nest, followed by a rapid decrease due to heavy mortality among the young and complicated by their dispersal. In late autumn and winter, other individuals leave the wood, particularly in a hard winter, and they or others return in early spring, before breeding. In

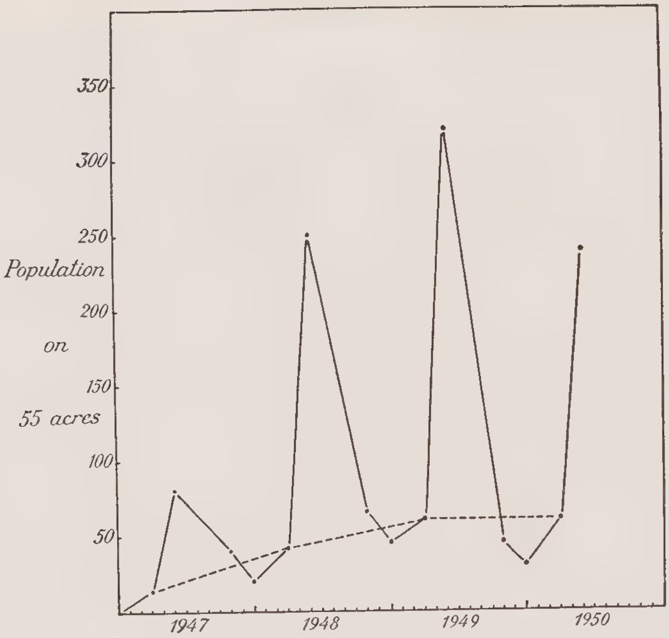


Fig. 5. Population changes in *Parus major* near Oxford (Gibb).

view of the complexity of such changes, workers taking long-term censuses in the future should aim to repeat them several times each year.

### *Irruption birds*

The "irruption" or "invasion" birds provide a rather special type of population change. At intervals, these birds move out in large numbers from their normal range into other areas where they are not usually seen. The best-known species of this type inhabit the northern coniferous forests, and the invasions of members of this group into or through North-east Prussia are summarised in Table 2. All of the species concerned depend for their winter food on one or a few species of fruits or seeds, while some of them e. g. *Loxia* and *Nucifraga*, depend on the same food for raising their young, though others, e. g. *Bombycilla* and *Dryobates,* feed their young primarily on insects. Despite what has sometimes been maintained (e. g. by Siivonen, 1941), the invasions of these birds do not occur at regular intervals, as can be seen from Table 2. Also, if the data for North-east Prussia are compared with those for other regions, such as Great Britain (Witherby *et al.*, 1938), Hungary (Warga 1935–38) or North America (Griscom, 1937; Speirs, 1939),

Table 2. Some Irruption Birds in N. E. Prussia (after Tischler (1941). Years of major invasions.

| *Nucifraga caryocatactes* | *Garrulus glandarius* | *Loxia curvirostra* | *Pinicola enucleator* | *Bombycilla garrulus* | *Dryobates major* |
|---|---|---|---|---|---|
| 1900 | — | — | — | — | — |
| — | — | — | — | — | — |
| — | — | — | — | — | — |
| — | — | — | — | 1903 | 1903 |
| — | — | — | — | — | — |
| — | — | — | — | — | — |
| — | — | — | — | — | — |
| 1907 | 1907 | — | — | — | — |
| — | — | — | — | — | — |
| — | — | 1909 | — | — | 1909 |
| — | 1910 | 1910 | — | 1910 | — |
| 1911 | — | — | — | — | — |
| — | 1912 | — | — | — | — |
| 1913 | — | — | 1913 | 1913 | — |
| — | — | — | — | — | 1914 |
| — | — | — | — | — | — |
| — | 1916 | — | — | — | — |
| 1917 | — | — | — | — | — |
| — | — | — | — | 1918 | — |
| — | — | — | — | — | 1919 |
| — | — | — | — | — | — |
| — | — | — | — | 1921 | — |
| - | — | - | — | — | - |
| — | — | — | — | 1923 | — |
| — | — | — | — | — | — |
| — | — | — | — | — | — |
| - | — | — | — | — | — |
| — | 1927 | — | — | — | — |
| 1928 | — | — | — | — | — |
| — | — | 1929 | — | — | 1929 |
| — | 1930 | — | — | — | — |
| — | — | — | — | 1931 | — |
| — | 1932 | — | — | 1932 | — |
| 1933 | — | — | — | — | — |
| — | — | — | — | — | — |
| — | — | 1935 | — | 1935 | 1935 |
| — | 1936 | — | — | — | — |
| — | — | — | — | 1937 | — |
| — | — | (1938) | 1938 | — | — |
| 1939 | 1939 | 1939 | — | — | 1939 |

*Note:* i) Also *Parus ater*, in unusually large numbers 1929 (1931) and 1935.
ii) Most of the above species occur in small numbers every year and the decision as to what constitutes a major invasion is somewhat arbitrary.

the apparent periodicity of the same species is seen to be different in different regions (e. g. *Loxia* and *Pinicola* in North America compared with Europe; *Bombycilla* in Hungary compared with Great Britain etc. etc.). Table 2 also shows that different species do not tend to irrupt in the same year, the only partial exception to this statement being that the species dependent on spruce (*Picea*) seeds may invade simultaneously (*Loxia curvirostra, Dryobates major, Parus ater*).

The invasions of the above species have sometimes been interpreted as a mechanism for destroying surplus numbers, a form of race suicide. This cannot seriously be maintained. First, Warga (1935–38) has shown that Waxwings (*Bombycilla garrulus*) ringed in the invasion areas in Hungary have later returned to the northern breeding grounds. Secondly, not only have local movements been linked up with local food shortage, notably in the Crossbill (*Loxia curvirostra*) by Reinikainen (1937), but the latter author also showed that the big Crossbill eruption of 1930 was correlated with a widespread failure of the spruce cone crop. Likewise Pynnönen (1939) found that the three large eruptions of the Great Spotted Woodpecker (*Dryobates major*) from Finland in the twentieth century were the three years when both pine and spruce cone crops were extremely poor. Food failure *per se* does not, however, provide an adequate explanation of all the facts. Thus the Crossbill has been found invading North-east Prussia as early as May, before the new spruce crop in the breeding grounds could have ripened. Again, Siivonen (1941) could attribute only the minor and not the major eruptions of the Waxwing to a failure of the berry crop in Finland. These latter facts are not, I suggest, irreconcilable with the view that potential food shortage is the ultimate reason why eruptions have survival value. Apparently, the immediate stimulus for a large eruption can be provided by high population density. Such a response would have survival value from the food point of view, for when the bird density is very high, even an average fruit crop might be inadequate to maintain them; further, when the bird density is high, the next fruit crop is likely to be below average, because a high density of the birds is presumably a result of high survival due to a good crop of fruit in the previous season, and the plants concerned (at least the conifers) do not usually have two good fruit years in succession.

Except that the irruption birds have a highly specialised vegetarian diet, and that they have a wandering habit stimulated by food shortage or high population density, I do not think that they present any novel principle of population dynamics; though their fluctuations, at least outside the normal breeding range, are perhaps larger than those of many birds. It should be stressed, however, that these species have been studied almost exclusively in the areas receiving the invasions. There is need for a detailed study of population changes and food availability within the normal range of the species, coupled with extensive ringing of adult and young birds, for a more precise determination of their movements.

The species erupting from the northern coniferous forests have been studied chiefly in Europe, and much less in North America. Irruption birds are also found in steppe and semi-desert regions in Asia, Africa and Australia (for the last see Serventy and Whittell, 1948); but except for the Rose-coloured Pastor (*Pastor roseus*) and its dependence on locust swarms (Schenk, 1929; Serebrennikov, 1931) these species have been little studied.

### *Four-year and ten-year cycles*

Some of the bird predators of arctic and subarctic regions show population changes and irruptive behaviour very similar to those of the species discussed in the previous section. Thus they have a wandering habit, moving from areas of food scarcity to food abundance, and when their food supply fails over a wide area, they move out in large numbers, and appear in regions where they are otherwise unknown. The main difference is that the predator invasions tend to come at regular and not irregular intervals, those from the tundra having a 3–4 year cycle, and those from the Hudsonian Zone (conifer forest) a 9–10 year cycle.

It is generally agreed that the fluctuations and wanderings of these predators are caused by the great changes in density of their chief prey. The correlation is most clearly established for the Snowy Owl (*Nyctea scandiaca*), which preys primarily on the lemming (*Lemmus* or *Dicrostonyx*) (Chitty, 1943, 1945; Shelford, 1945). There is an extensive literature, summarised by Elton (1942), showing the existence of a similar 3–4 year cycle in various other tundra species. Some of these, however, such as the Rough-legged Buzzard (*Buteo lagopus*), feed much on voles (*Microtus*), and the prey preferences of these other species on the breeding grounds need much more detailed study. The same applies to the two American species of the Hudsonian Zone which invade every 9 or 10 years, namely the Goshawk (*Accipiter gentilis*) and Horned Owl (*Bubo virginianus*), which come from the region where the Varying Hare or Snowshoe Rabbit (*Lepus americanus*) and various gallinaceous birds show a 9–10 year cycle. It is significant that in Norway, where they are in the region of the 3–4 year cycle, both Goshawk and Eagle Owl (a *Bubo* species closely related to *B. virginianus*) show a 3–4 year cycle, and not a cycle of 9–10 years as in Canada (compare Tables

Table 3. **Four-year Cycle in South Norway.**

| Years of peak population in | | | | |
|---|---|---|---|---|
| *Lemmus lemmus* | *Vulpes* and *Alopex* | *Buteo lagopus* | *Accipiter gentilis* | *Lagopus lagopus* |
| 1871–2 | — | 1872 | 1871–3 | 1872 |
| 1875–6 | — | 1875 | 1876 | 1876 |
| 1879–80 | 1880 | 1879–80 | 1880 | 1880 |
| 1883–4 | 1884 | 1883–4 | 1883–4 | 1883 |
| 1887–8 | 1887 | 1887–8 | 1889 | 1887 |
| 1890–1 | 1892 | 1891 | 1891 | 1891 |
| 1894–5 | 1895 | 1894–5 | 1895 | 1895 |
| 1897 | 1899 | 1898–9 | 1899 | 1897 |
| 1902–3 | 1903 | 1902 | 1901–2 | 1903 |
| 1906 | 1907 | 1906 | 1905–6 | 1906 |
| 1909–10 | 1910 | 1909–10 | 1911–12 | 1908–9 |
| — | — | — | — | 1911–12 |

*Note:* Data on *Lemmus, Vulpes* and *Lagopus* from Elton (1942), *Vulpes* derived from Johnsen (1929) and *Lagopus* from Kloster (1928); data on *Buteo* and *Accipiter* from Johnsen (1929) calculated by me from the figures in his Appendix for the area worked by Kloster.

3 and 4). This strongly corroborates the view that food supply is the basic cause of the predator cycles. It may be added that not only do the predatory birds move out of areas where their prey is scarce and into areas where it is abundant, but they lay abnormally high clutches when their prey is particularly abundant.

It is remarkable that not only the predatory birds, but also the common gallinaceous birds of the north, seem to follow the lemming or hare cycle. Table 3, for instance, shows that in Norway the Willow Grouse (*Lagopus lagopus*) has a 3–4 year cycle like the lemming, while Table 4 shows that in North America the Ruffed Grouse (*Bonasa umbellus*), and other species of grouse, have a 9–10 year cycle like the Varying Hare. This correlation has usually been explained by supposing that the gallinaceous species are affected by the same climatic factors that cause the lemming or hare cycle. However, the view that these cycles are caused by some general climatic factor seems disproved by the discovery, confirmed by workers on several species, that the cycle is not synchronous throughout the range. In different parts of North America, for instance, the four-year cycle has been found to be up to two years out of step, and the ten-year cycle up to five years out of step, this of course being the maximum diver-

Table 4. Ten-year Cycle in South-Central Canada and North-Central U.S.A.

| *Lepus americanus* | *Lynx canadensis* | *Accipiter gentilis* | *Bubo virginianus* | *Bonasa umbellus* | *Pedioecetes phasianellus* |
|---|---|---|---|---|---|
| 1857 | 1857 | — | — | 1857 | — |
| 1865 | 1866 | — | — | 1866 | — |
| 1876 | 1876 | — | — | 1877 | — |
| 1887 | 1885–6 | 1886 | 1887 | 1887 | — |
| 1896 | 1895 | 1896, 97 | 1897 | 1898 | — |
| 1905 | 1905 | 1906 | 1907 | 1906 | 1902–03 |
| 1914 | 1913–14 | 1916, 17 | 1916 | 1914–15 | 1912–13 |
| 1924 | 1925 | 1926, 27 | 1927 | 1923 | 1923 |
| 1934 | 1935 | 1934, 35 | 1936 | 1933 | 1933 |
| 1943 | — | — | — | 1942 | 1942 |

*Note:* (i) *Lepus* from MacLulich (1937) modified by Elton and Nicholson (1942); *Lynx* from Elton and Nicholson (1942); *Accipiter* and *Bubo* from Speirs (1939) and Bump *et al.* (1947 p. 324); *Bonasa* before 1900 from Schorger (1947) and after 1900 from Bump *et al.* (1947 p. 566) and Grange (1948); *Pedioecetes* from Criddle (1930) and Grange (1948).

(ii) The *Lepus* and *Lynx* data refer to the peak catches in the main Hudson Bay Co. region of Canada; the *Accipiter* and *Bubo* data to invasions of Toronto and northeastern U.S.A. from regions further north; the *Bonasa* data before 1900 to peaks in Wisconsin and after 1900 to the commonest peak year for the districts in Canada and U.S.A. around the Great Lakes; the first three *Pedioecetes* figures to Manitoba and the last two to Wisconsin.

(iii) As there are local differences of several years in the time of the peak, and as the data given above have had to be taken from rather different regions in different species, *the data for different species are not directly comparable.* They merely give a general indication.

gence possible (e. g. Clarke, 1936, and Bump *et al.*, 1947, for *Bonasa umbellus,* Chitty and Elton, 1940, for *Lepus americanus,* and Chitty, 1943, 1945, for the lemming, etc.).

As an alternative hypothesis, I would suggest that the cycle of lemming or hare is the primary one (the cause of which is outside the scope of this review), and that the cycle of the gallinaceous birds is in some way caused by that of the rodent. This suggestion is strongly supported by Table 5, which shows the successive peaks in the cycle of the Willow Grouse (or Ptarmigan) *Lagopus lagopus.* In Norway, the peaks are 3–4 years apart like those of the lemming. On the North Shore of the Gulf of St. Lawrence they are about 10 years apart, like those of the Varying Hare. Further, the Red Grouse (*L. scoticus*), a pronounced geographical form of the same species, occurs in Britain, where both lemming and Varying Hare are absent, and here the interval between peaks is about 6 years.

Table 5. *Lagopus* Peaks in Different Regions.

| *L. lagopus* | | *L. scoticus* |
|---|---|---|
| North Shore St. Lawrence | South Norway | Scotland |
| — | — | 1858 |
| 1863-4 | — | — |
| — | — | 1865 |
| 1872–3 | 1872 | 1872 |
| — | 1876 | 1876 |
| — | 1880 | — |
| — | — | 1882 |
| 1883-5 | 1883 | — |
| — | — | 1886 |
| — | 1887 | — |
| — | 1891 | — |
| — | — | 1894 |
| 1895 | 1895 | — |
| — | 1897 | — |
| — | — | 1901 |
| 1903–4 | 1903 | — |
| — | 1906 | — |
| — | — | 1907 |
| — | 1908–9 | — |
| Average 10 years | Average 3.4 years | Average 6.1 years |

*Note:* (i) Data for St. Lawrence from Comeau (1909), for Norway from Kloster (1928) as cited by Elton (1942), and for Scotland from Leopold and Ball (1931) analysing the data in *The Grouse in Health and Disease* (1911). North Shore St. Lawrence is in zone of *Lepus americanus* (9–10 year cycle), Norway of *Lemmus lemmus* (3–4 year cycle), and Scotland of no dominant rodent.

(ii) See also Braestrup (1941) for peaks of *Lagopus mutus* in Greenland where *Lemmus* absent; average apparently 4.4 years, but very erratic—apparent peaks in S. W. Greenland 1889, 1892, 1894, 1901, 1904, 1910, 1914, 1918, (1922), 1924, 1927, 1937.

How a population cycle in a rodent might result in a similar cycle in a gallinaceous species in the same region is not clear. Disease seems ruled out, for though disease has sometimes been common during a grouse decline, it is not always the same disease (see, for instance, Edminster, 1947), and there is no reason to think that some disease spreads from the rodent to the gallinaceous bird. In any case, Green *et al.* (1939) indicate that the disease of the Varying Hare during a crash is probably a deficiency and not an infectious disease. This might suggest that, when the rodent is extremely abundant, it might adversely affect the food supply of the gallinaceous bird.

However, the Varying Hare and Ruffed Grouse take quite different foods and though both lemming and *Lagopus* eat berries, berries are not the main food of either animal. Hence food also seems ruled out.

It therefore seems worth enquiring whether predators might not constitute the link between the two cycles. The predator density rises rapidly as the rodents increase, and though it is generally agreed that predators do not become sufficiently abundant to be the cause of the rodent crash, their effect on the gallinaceous birds when the rodents decline might not be negligible. Several of the commonest predators on lemming or Varying Hare are known to take gallinaceous birds as a favourite alternative. Further, the few available figures suggest that the peak density of the dominant rodent is far higher than that of the gallinaceous birds. Thus the peak density of the Varying Hare may be more than 10 to the acre (MacLulich, 1937, especially p. 121), but that of *Bonasa* is at the most only about one bird to 4 acres. (Bump *et al,* 1947). Again, the figures for animals shot in Wisconsin show that the minimum for hares was actually higher than the maximum for grouse (Grange, 1948). If the gallinaceous birds have a density which is only about one-fortieth of that of the dominant rodent, the predators which depend primarily on the rodent might well have a serious effect on the gallinaceous population in times of rodent scarcity. This possibility requires testing in the field. An easy point to test is whether the decline of the gallinaceous bird *always follows* that of the rodent, a point which I cannot satisfactorily determine from the literature.

As regards future research on cycles, there is an obvious need to make precise measurements of the operative factors in some northern area which experiences a strongly marked cycle. These precise measurements should include the population density of the rodent, of the predators and of the gallinaceous birds, as until now the fluctuations have been assessed either from numbers trapped or shot, or from general statements of abundance. They should also include an accurate quantitative assessment of the effects of predation on each prey animal. The food requirements of each animal, and the availability of its food, must also be measured. Such measurements are needed at every stage of the cycle, and extending over at least two full cycles. While they are badly needed for some subarctic Continental area, parallel study on an island off the coast, and in any area where the dominant rodent is absent, would also be of great value.

### *Changes in range*

As time is limited, I will merely mention that important studies have been made recently on changes in range (sometimes involving abundance too) in various birds—see the papers by Fisher on the Fulmar (*Fulmarus glacialis*) in the North Atlantic, and by Merikallio on certain passerine birds in north Finland, given at this Congress. Merikallio and Kalela (1949 *et al.*) have analysed range changes in relation to changes in climate and other factors.

### *Conclusion regarding general population surveys and censuses*

. From this survey of the general population studies so far undertaken in birds, I would provisionally suggest that, while further censuses will corroborate the existence of restricted fluctuations of various types, they are not very likely to elucidate the factors involved. For the latter, I suggest that it may prove more profitable to split up the problem, studying one aspect in one species, another in a different species, wherever conditions seem easiest. Ideally, it would be better to study every aspect in one and the same species, but field study of population problems is so difficult that it is unlikely that one species will provide suitable opportunities for the study of all aspects. At the present time, therefore, division and analysis seems a more suitable method of approach than an over-all study. Before passing on to the second half of this review, I would also stress the need for ornithologists to compare their population studies with those being undertaken in insects, fish and other animals, and to familiarise themselves with the procedure, methods and theories being developed by workers in the other groups concerned.

## Part II. Factors involved

### *Reproduction and mortality*

Population density is determined by (a) reproductive rate, and (b) mortality. Either of these might be density-dependent, and either might therefore be concerned in producing the restricted fluctuations which we call the natural regulation of populations. At least in birds, however, I think it very unlikely that the major regulation is achieved through the reproductive rate. Average clutch-size may vary a little from one year to the next but, in most species at least, it is little affected by population density. The evidence suggests that birds reproduce as rapidly as they can, and that the rate is much higher than that essential to replace losses in an average year. The last point is illustrated by the rapid recovery shown by nearly every species after a set-back, a rate of increase which is not maintained once the population is back to a high density, although the clutch-size is usually similar at both low and high densities (see, for instance, Fig. 2). I consider that regulation is achieved mainly by variations in the mortality-rate, which rises as population density rises. The normal high annual mortality in birds is, in fact, a result of their high reproductive rate, and the view that clutch-size has been adjusted to fit the mortality of the species cannot be seriously maintained (Lack, 1947–48).

### *Breeding Seasons*

The problem of breeding seasons will not be reviewed here, as it has been the subject of a symposium in the *Ibis* for April 1950, edited by R. E. Moreau. The papers in this symposium show clearly that birds tend to breed at that season of the year when food for their young is most abundant. The needs for further research in this field are:

i) a closer study of breeding seasons and food supply in tropical rain-forest, the one major habitat in which evidence for the above correlation is still unsatisfactory;

ii) precise quantitative measurements of both breeding season and food density in all types of habitats, in the manner shown in Fig. 6 for Great Tit (*Parus major*) and Blue Tit (*P. caeruleus*) and their caterpillar food near Oxford (after Gibb, 1950). The two titmice species feed their young primarily on defoliating caterpillars (mainly *Cheimatobia brumata*), the abundance of which was measured by the amount of their excrement falling per day on to trays placed on the forest floor. (To facilitate comparisons, both caterpillar abundance and the number of pairs of tits with nestlings were scaled to a peak value of 100 in each year.)

### *Clutch-size*

The problem of clutch-size was also reviewed recently in the *Ibis* (Lack, 1947–48), so I will here merely refer to my view that clutch-size is not normally determined by the physiological capacity of the bird; nor is it adjusted to the mortality of the species. Instead, it is adapted to the average maximum number of young that the parents can raise. Circumstantial evidence in favour of this last view includes a geographical trend of increasing clutch-size with increasing latitude (and hence daylength), and a seasonal trend of increasing clutch-size from early spring to midsummer with a decline thereafter (again corresponding to daylength). These trends, also the evidence from parasitic birds, and the probable function of asynchronous hatching in birds of prey, were discussed at length in the *Ibis* review (Lack, *loc. cit.*).

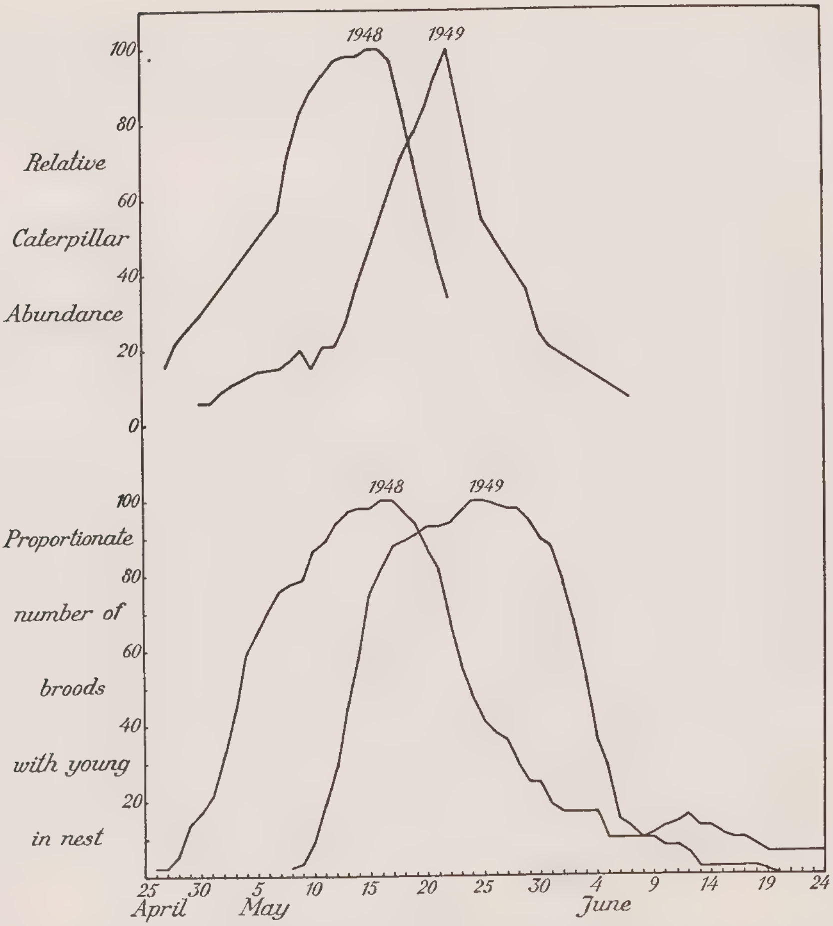


Fig. 6. Caterpillar abundance (above) and Tit Breeding Season (below) near Oxford (after Gibb).

In all the species so far investigated, hatching success has been found to be independent of clutch-size, as shown in the Partridge (*Perdix perdix*) in Table 6.

The disadvantage of a larger clutch-size is that each nestling receives less food. As shown in Table 7 for various African species, with a brood of larger size the parents tend to increase their feeding frequency, but not proportionately, hence each nestling in a large brood receives proportionately less than each nestling in a small brood. It should be stressed that there are marked individual differences in feeding frequency, so that, to test the above point, a large series of observations is needed.

Table 6. Hatching Success in *Perdix perdix*,

| Clutch-size | No. of eggs | % hatched |
|---|---|---|
| 8 | 120 | 91 |
| 9 | 351 | 88 |
| 10 | 1 080 | 91 |
| 11 | 1 716 | 91 |
| 12 | 5 340 | 90 |
| 13 | 5 681 | 90 |
| 14 | 9 324 | 90 |
| 15 | 10 650 | 91 |
| 16 | 9 552 | 91 |
| 17 | 6 052 | 90 |
| 18 | 4 104 | 90 |
| 19 | 1 520 | 91 |
| 20 | 840 | 91 |
| 21–29 | 831 | 92 |
| Total | 57 202 | 90.4 |

*Note:* Details in Lack (1947 b).

Table 7. Feeding Frequency in relation to Brood-size.

| | Brood-size | Feeding visits per hour | |
|---|---|---|---|
| | | Total | Per young |
| *Ptyonoprogne fuligula* | 1 | 12 | 12 |
| | 2 | 18 | 9 |
| | 3 | 26.4 | 8.8 |
| *Hirundo abyssinica* | 2 | 12.4 | 6.2 |
| | 3 | 15 | 5 |
| *Hirundo smithii* | 1 | 16 | 16 |
| | 2 | 26.4 | 13.2 |
| | 3 | 25.5 | 8.5 |
| *Psalidoprocne holomelaena* | 1 | 3.1 | 3.1 |
| | 2 | 4.4 | 2.2 |
| *Cypsiurus parvus* | 1 | 1.1 | 1.1 |
| | 2 | 1.86 | 0.93 |
| *Micropus caffer* | 1 | 0.46 | 0.46 |
| | 2 | 0.94 | 0.47 |
| *Colletoptera affinis* | 1 | 0.52 | 0.52 |
| | 2 | 0.74 | 0.37 |
| | 3 | 0.99 | 0.33 |

*Note:* After Moreau (1947).

Table 8. Fledging Success of *Apus melba*.
(Omitting late broods.)

| Size of brood hatched | No. of young | Percent flying | Productivity per brood |
|---|---|---|---|
| 1 | 58 | 97 % | 1.0 |
| 2 | 562 | 87 % | 1.8 |
| 3 | 1 623 | 79 % | 2.4 |
| 4 | 20 | 60 % | 2.4 |

*Note:* Details in Lack and Arn (1947).

Table 9. Nesting Success of *Sturnus vulgaris* in Holland.
(Omitting complete losses.)

| Clutch-size | Eggs laid | Young flying | % flying |
|---|---|---|---|
| 2 | 16 | 14 | 82 % |
| 3 | 105 | 86 | 82 % |
| 4 | 864 | 727 | 84 % |
| 5 | 2 770 | 2 324 | 84 % |
| 6 | 2 184 | 1 784 | 82 % |
| 7 | 756 | 620 | 82 % |
| 8 | 112 | 87 | 78 % |

*Note:* Details in Lack (1948 a), using data from Kluijver (Wageningen).

The decrease in the food received by each nestling as brood-size rises might be expected to produce a rise in nestling mortality with increasing brood-size. The latter is sometimes the case, as shown in Table 8 for the Alpine Swift (*Apus melba*). Indeed, the data suggest that 3, which is the commonest clutch-size in this species, is also the optimum family-size, and that, if the parents start with a larger number, they cannot in fact raise more fledglings.

In various passerine birds, unlike swifts, nestling mortality does not increase with increasing brood-size. This is shown for the Starling (*Sturnus vulgaris*) in Table 9 and for four species of Turdidae elsewhere (Lack, 1949b). It might therefore be thought that, in passerine birds, broods of larger size are not penalised; but appearances are misleading. In passerine birds the weight of the young at the time of leaving the nest is very variable (Lack and Silva, 1949), hence undernourishment in the nest might influence the

Table 10. Post-fledging Survival of *Sturnus vulgaris* in Switzerland.

| Brood-size | Number ringed as young | Percent recovered over 3 months old | Productivity (Percent recovered × brood size) | Percent recovered 1–2 months old |
|---|---|---|---|---|
| 1 | 65 | — | — | |
| 2 | 328 | 1.8 | 3.7 | .21 |
| 3 | 1 278 | 2.0 | 6.1 | |
| 4 | 3 956 | 2.1 | 8.3 | |
| 5 | 6 175 | 2.1 | 10.4 | .35 |
| 6 | 3 156 | 1.7 | 10.1 | .43 |
| 7 | 651 | 1.5 | 10.2 | |
| 8 | 120 | 0.8 | | |
| Total | 15 757 | 1.94 | — | .32 |

*Note:* Details in Lack (1948 a), using data from Vogelwarte Sempach.

chances of subsequent survival. Table 10 shows that, in fact, in the Starling (*Sturnus vulgaris*) the proportion of individuals which survive their first three months after leaving the nest is higher among the young from broods of small than large size (see especially third column of table). Indeed, proportionate mortality rises so rapidly with increasing brood-size that a brood of 5, 6 or 7 young gives rise to an equal number of eventual survivors (fourth column of Table 10). One can therefore see why natural selection would operate in favour of 5 as the commonest clutch-size for first broods of the Starling in the region concerned. The mortality in question was measured indirectly, through analysing the original brood-size of those ringed Starlings recovered after they were at least three months old, and comparing it with the numbers of each brood-size originally ringed. A check is available through analysing the original brood-size of the young Starlings found dead within two months of leaving the nest, and, for these, it was found that proportionately more came from large than small broods (right-hand column of Table 10).

In the other passerine species so far investigated, the relation between post-fledging mortality and brood-size has been found to be less clear-cut than in the Starling (Lack, 1949b for Turdidae, and *Evolution in press* for *Parus major*). In such species, I have suggested that clutch-size is modifiable and adaptive, so that clutches of larger size tend to be laid when conditions are more favourable, and clutches of smaller size when they are less favourable, for raising young. Under these circumstances, survival would not necessarily be poorer from the larger broods.

Important problems for future research in this field are:

i) quantitative study of local, seasonal and annual differences in average clutch-size in a passerine species with a very modifiable clutch-size, the study to be made in several localities simultaneously and over several years, and linked with measurements of juvenile survival and availability of food for the young;

ii) large-scale study of clutch-size, nestling survival and food density in a bird of prey; this would need to extend over several years because in this group nestling mortality, and in some species clutch-size, varies markedly with the density of the food supply;

iii) study of nestling survival in relation to brood-size in tropical passerine birds, particularly to test the suggestion of Skutch (1949) that, with a larger brood, the more frequent visits of the parents with food may render the nest more conspicuous to predators;

iv) enquiry into clutch-size in ducks, in which clutch-size seems as constant as in most other birds, but, since the parents do not feed the young and newly hatched broods may merge, the views developed here for other birds seem not to apply;

v) experimental analysis of the genotypic and phenotypic factors modifying clutch-size.

### *Annual mortality*

Since, in a stable population, the death-rate is equal to the birth-rate, most species of birds must have a high annual mortality, and one would expect their average age to be low. This point has been investigated by three methods. First, the individuals of a species living in a given area have been caught and colour-ringed, and their subsequent survival or return has been observed, as for instance in the Redstart (*Phoenicurus phoenicurus*) in Table 11. In such studies, it is assumed that those colour-ringed individuals which fail to re-appear have in fact died. Almost certainly, a proportion of them will have shifted, not died, though this proportion, and the resulting error, may be small.

Secondly, using the data of some national bird-ringing scheme, the average age can be calculated of all those individuals later reported dead. The proportion recovered is small, only 1 or 2 per cent in many passerine birds, hence the sample may not be typical, as regards age, of the population as a whole; but the possible error from this source seems unlikely to be serious except in

Table 11. Survival of *P. phoenicurus* in Holland.

| Year ringed | Number of ringed birds present | | | | |
|---|---|---|---|---|---|
| | 1935 | 1936 | 1937 | 1938 | 1939 |
| 1935 | 93 | 35 | 18 | 6 | 0 |
| 1936 | . | 65 | 20 | 9 | 4 |
| 1937 | . | . | 66 | 22 | 12 |
| 1938 | . | . | . | 49 | 19 |

Average annual survival = 145/383 = 38 %
Hence adult to juvenile ratio = 38 : 62 = .61
Compare adult to juvenile ratio on Mellum 3 : 5 = .60

*Note:* after Ruiter (1941); Mellum figures from Goethe (1939).

Table 12. Survival of British-ringed *Vanellus vanellus.*

| Year (from Jan. 1st after ringing) | Alive at start | Found dead | % dying during year |
|---|---|---|---|
| 1st | 593 | 198 | 33 % |
| 2nd | 395 | 134 | 34 % |
| 3rd | 261 | 90 | 34 % |
| 4th | 171 | 51 | 30 % |
| 5th | 120 | 48 | 40 % |
| 6th | 72 | 23 | 32 % |
| 7th | 49 | 21 | 29 % |
| 8th | 28 | 9 | 32 % |
| 9th | 19 | 6 | 32 % |
| 10th–14th | — | 13 | — |

Average annual mortality = 593/1733 = 34 %.

*Note:* Based on all young ringed in Britain before 1940 and later recovered, excluding those found before their first January 1st of life; original analysis for this paper.

The older individuals include 5 in the 10th, 6 in the 11th, 1 in the 12th and 1 in the 14th year.

a) those species which tend to lose their rings with increasing age (notably sea-birds, through corrosion),

b) those species in which many recoveries are due to shooting (in which case the sample tends to include too high a proportion of juvenile and inexperienced birds), and

c) those species in which the juveniles migrate more than the adults and the chance of rings being reported is much higher in some countries than others.

Table 13. Annual Adult Mortality in Various Species.

| Species | Method (See note i) | Number studied | Average annual adult mortality | Average expectation of further life | Region | Reference (* recalculated by Lack) |
|---|---|---|---|---|---|---|
| *Corvus frugilegus* | D | 54 | 47 % | 1.6 yrs. | France | Bourlière (1947)* |
| *Sturnus vulgaris* | L | 253 | 52 % | 1.4 " | Holland | Kluijver (1935) |
| *Sturnus vulgaris* | D | 197 | 52 % | 1.4 " | England | Lack & Schifferli (1948) |
| *Sturnus vulgaris* | D | 306 | 63 % | 1.1 " | Switzerland | Lack & Schifferli (1948) |
| *Melospiza melodia* ♂♂ | L | 101 | 45 % | 1.7 " | U.S.A. | Nice (1937) |
| *Melospiza melodia* ♂♂ | J:A | 115 | 44 % | 1.8 " | U.S.A. | Nice (1937) |
| *Parus major* | D | 64 | 46 % | 1.7 " | Switzerland | Plattner *et al.* (1946–7) |
| *Muscicapa hypoleuca* ♂♂ | L | 189 | 54 % | 1.4 ' | Finland | v. Haartman (1949)* |
| *Turdus merula* | D | 258 | 42 % | 1.9 " | England | Lack (1946b)* |
| *Turdus ericetorum* | D | 262 | 47 % | 1.6 " | England | Lack (1946b)* |
| *Turdus migratorius* | D | 597 | 48 % | 1.6 " | U.S.A. | Farner (1949) |
| *Erithacus rubecula* | D | 129 | 62 % | 1.1 " | England | Lack (1948b) |
| *Phoenicurus phoenicurus* | L | 273 | 62 % | 1.1 " | Holland | Ruiter (1941) |
| *Hirundo rustica* | D | 99 | 63 % | 1.1 " | England | Lack (1949d) |
| *Apus apus* | T | 266 | 20 % | 4.6 " | Sweden | Magnusson *et al.* (1948) |
| *Apus apus* | L | 18 | 18 % | 5.1 " | Switzerland | Weitnauer (in litt.)* |
| *Anas platyrhyncha* | D | 305 | 65 % | 1.2 " | England | Höhn (1948) |
| *Ardea cinerea* | D | 60 | 31 % | 2.7 " | England | Lack (1949c) |
| *Scolopax rusticola* | D | 89 | 37 % | 2.2 " | England | Lack (1943b) |
| *Vanellus vanellus* | D | 593 | 34 % | 2.4 " | England | Lack (original) |
| *Vanellus vanellus* | D | many | 40 % | 2.0 " | N.W. Europe | Kraak *et al.* (1940) |
| *Vanellus vanellus* | J:A | 434 | 40 % | 2.0 " | Holland | Klomp (1946) |
| *Charadrius hiaticula* | L | 37 | 46 % | 1.7 " | Germany | Laven (1940) |
| *Sterna hirundo* | T | many | 30 % | 2.8 " | U.S.A. | Austin (1942)* |
| *Larus argentatus* | D | 349 | 30 % | 2.8 " | U.S.A. | Paynter (1947)* |
| *Lophortyx californica* | J:A | 624 | 50 % | 1.5 " | U.S.A. | Emlen (1940) |

*Note:* (i) L = return of live colour-ringed birds; D = sample of ringed birds recovered dead; T = trapped sample; J: A = juvenile to adult ratio.

(ii) For calculation of average annual adult mortality see Lack and Schifferli (1948). When an author did not give this average, I have calculated it from his published data. The following points should also be noted:

*Corvus frugilegus:* data converted from each 400 to 365 days, first 400 days omitted.

*Melospiza melodia:* for return of live birds, I used only the first three years of Nice's study, as the habitat was later disturbed and some birds probably shifted. For juvenile to adult ratio, I used all six years, taking right hand columns of Table 25 in Nice, 1937 (p. 176).

*Muscicapa hypoleuca:* Von Haartman found 37.1 % of males returned and he assumed that this represented all those still alive. The latter is not so, for his data show that of those males present at least three years, 5 out of 37 (13.5 %) were missed in at least one intervening year.

The sample recovered from British-ringed Lapwings (*Vanellus vanellus*) is analysed for age in Table 12. This shows that the average annual adult mortality is constant at all ages up to the time when extremely few individuals are left alive, and the same holds for the other species so far investigated. The average life of a bird is far shorter than its potential age, and extremely few die of "old age." This is in marked contrast to the type of life-curve found in laboratory populations of animals, or in mankind in western civilisation during the last hundred years (Lack, 1943a).

In a stable population, the number of young individuals breeding for the first time must be equal to the number of adults lost during the previous year. Hence an assessment of the ratio of first-year to older breeding birds provides a third way of estimating the annual adult mortality. The counts must, of course, be made over several years to allow for annual variations. This method could be more widely used than it has been, though it is restricted to those species in which the older individuals can be distinguished by their appearance from those breeding for the first time; and it cannot be used for those species in which a proportion of the juveniles fail to return to the breeding grounds, or in which the age of first breeding varies with the individual.

The average annual adult mortality, and the average expectation of further life of an adult (loosely called the "average age"), are summarised in Table 13 for all those species of birds in which a large sample has been analysed. It is satisfactory to notice that in several cases where the mortality has been calculated by two independent methods the results approximately agree. Thus the ratio of juvenile to adult Redstarts (*Phoenicurus phoenicurus*) observed on spring migration at Mellum fits the figures based on a colour-ringed population in Holland in Table 11. Again, a figure based on the return of living ringed birds fits one based on a sample of birds recovered dead in the Starling (*Sturnus vulgaris*), while a figure based on the juvenile to adult ratio fits one based on live returns in the Song Sparrow (*Melospiza melodia*) and one based on a sample of birds recovered dead in the Lapwing

---

This gives a very rough idea of the proportion shifting, which I have used as a correction factor. Hence percentage alive one year later $= 37.1 + (0.135 \times 62.9) = 46\ \%$.

*Apus apus:* Weitnauer sent data amplifying published work.

*Sterna hirundo:* result read off graph; see notice of my review under Austin (1942) in references to this paper.

*Larus argentatus:* recalculated by me to allow for different total banded each year, which affects chances of recovery of individuals from each age-group. The result differs by only 1 % from that based on best year only in Paynter, 1949.

*Lophortyx californica:* combined April, May, June average.

**Table 14. Relation between Reproductive Rate and Mortality in *Sturnus vulgaris*.**

| | Switzerland | England |
|---|---|---|
| Average May brood | 4.5 | 3.9 |
| Average late brood | 4.0 | 3.0 |
| % late broods | 33 % | 25 % |
| Productivity per pair | $\boxed{5.8}$ | $\boxed{4.7}$ |
| Average annual mortality | $\boxed{63\ \%}$ | $\boxed{52\ \%}$ |
| Expectation of further life in years | 1.1 | 1.4 |

*Note:* Derived from Lack and Schifferli (1948).

(*Vanellus vanellus*). It may be added that the figures for the annual mortality in Table 13 are in no case unreasonable in view of what is known of the reproductive rate and juvenile losses of the species concerned.

Since in a stable population the reproductive rate and the annual mortality must balance each other, it is to be expected that those species with a comparatively low reproductive rate will also have a low annual mortality. It is therefore interesting to see in Table 13 that the Swift (*Apus apus*), which has an unusually low clutch-size and nesting success, has a lower annual adult mortality than any other species so far studied. The same point is demonstrated in Table 14 for two populations of the same species. In the Starling (*Sturnus vulgaris*), both the reproductive rate and the annual mortality are higher in Switzerland than in England.

In all the studies so far undertaken, it has been found that the juvenile individuals have a rather higher mortality-rate, and a rather lower expectation of further life, than the adults, presumably due to their inexperience. In three species, there are enough figures to show the progressive improvement in juvenile survival as the birds get older. The figures are set out in Table 15 for the California Quail (*Lophortyx californica*) and the Lapwing (*Vanellus vanellus*), while for a similar analysis for the Starling (*Sturnus vulgaris*) see Lack and Schifferli (1948).

The two sexes may also differ in their mortality-rates, and when this is so, it will usually lead to an unequal sex-ratio in the population. The existance of such an unequal mortality-rate, tending to intensify the unequal sex-ratio with increasing age, is shown for three species of North American ducks in Table 16. On the other hand, in the Starling (*Sturnus vulgaris*), Kluijver (1935) found that the mortality-rate in adults of the two sexes was the same.

Table 15. Change in Juvenile to Adult Ratio with increasing Age, indicating progressive Improvement in juvenile Survival.

| Month | *Lophortyx californica* | | *Vanellus vanellus* | |
|---|---|---|---|---|
| | Total | Percent juvenile | Total | Percent juvenile |
| Aug. | — | — | 41 | 73 % |
| Sept. | — | — | 39 | 59 % |
| Oct. | 440 | 70 % | 44 | 50 % |
| Nov. | 1 042 | 62 % | 68 | 47 % |
| Dec. | 1 004 | 62 % | 152 | 36 % |
| Jan. | 482 | 58 % | 154 | 35 % |
| Feb. | 436 | 56 % | 106 | 39 % |
| Mar. | 229 | 54 % | 99 | 35 % |
| Apr. | 207 | 52 % | | |
| May | 222 | 52 % | 48 | 21 % |
| June | 195 | 45 % | | |

*Note: Lophortyx* distinguished by plumage (Emlen, 1940), *Vanellus* by ring number (Lack, original analysis).

Table 16. Change in Sex Ratio of Ducks with increasing Age.

| | When ringed | | At least 4 years later | |
|---|---|---|---|---|
| | Total | Percent male | Total | Percent male |
| *Dafila acuta* ......... | 23 674 | 66 % | 530 | 72 % |
| *Nyroca collaris* ....... | 6 116 | 77 % | 155 | 83 % |
| *N. affinis* ........... | 8 356 | 69 % | 160 | 77 % |

*Note:* After McIlhenny (1940).

Two obvious needs for further research on mortality-rates are:—

i) A study over as large an area as possible, and over as many years as possible, of a colour-ringed population of a sedentary species, checks being made at repeated intervals throughout the year to determine the seasons at which most individuals disappear. All previous studies of colour-ringed populations have had some other object, usually behaviour, as their primary aim. If population changes were made the primary object of study, a much larger population could be investigated, and, the larger the study area, the smaller the losses due to birds wandering;

ii) A study of mortality-rates in petrels (Procellariformes), as these birds appear to have an even lower reproductive rate than swifts, and may be expected to have a higher average life than any other species. It will be necessary to devise a type of bird ring or other mark which does not tend to get lost with increasing age, through corrosion in salt water or for any other reason.

### *Causes of mortality*

The causes of mortality are extremely difficult to observe. The watcher can usually record only the disappearance, not the death of his birds. Most die undetected. Further, even when the manner of death is seen, its true cause may be hard to assess. A bird may, for instance, be very short of food, and so may catch a disease, and so may be weakened and caught by a predator, and the observer will perhaps see only the last of these events.

In birds, the mortality factors which seem most likely to vary with population density, and which might therefore regulate it, are (a) food shortage, (b) predation, (c) disease, and (d) behaviour.

Discussing these in the reverse order of that listed, *behaviour* can be very important. Thus birds often move out if food becomes short, and may move in when food is unusually abundant. There are regular seasonal migrations, and less regular irruptions. There is also the disputed question of whether territorial behaviour effectively limits population density and, if it does, whether the limit is of survival value in relation to food supply. Behaviour factors must be kept constantly in mind by the ecologist, though they provide secondary rather than primary limitations to population density, and, if they have survival value, it is because they are related to food supply or to some other primary factor.

Many *diseases* of wild birds have been described, but their impact, if any, on population density has been seriously considered in only one case. As long as forty years ago, Leiper (1911) postulated that the nematode *Trichostrongylus pergracilis*, parasitic on the Red Grouse (*Lagopus scoticus*), constituted a delayed density-dependent mortality factor. This point should be re-investigated over several grouse cycles. American workers do not find any disease constantly associated with the periodical declines of the Ruffed Grouse (*Bonasa umbellus*) (Bump *et al.*, 1947; Edminster, 1947). The Red Grouse may, however, be in a peculiar position owing to the particularly drastic removal of its predators, and to other intensive management practice by man. Outside the gallinaceous birds, the relation of disease to population density has not been studied. To hazard a guess where all is unknown, I would suggest that in most birds disease will, if serious at all, be found to be a secondary rather than a primary factor limiting density.

As regards *predation*, while there are many qualitative lists of the birds taken by predators, there is as yet only one quantitative study relating predation to population density and total mortality. Tinbergen (1946) estimated that, in certain passerine species, the proportion of the mortality due to the Sparrowhawk (*Accipiter nisus*) was quite large, the figures for his four key species being given in the footnote to Table 17. These high proportions suggest that predation might be important in regulating population density in the passerine species concerned. The figures must, however, be accepted with caution, as Tinbergen's study related to only a very few pairs of Sparrowhawks, to only three years, and primarily to one season of the year, the summer at that; also some of the important steps in his quantitative assessments had inevitably to be based on uncertain assumptions and not on field measurements. His pioneer paper nevertheless represents a marked advance, and other such studies are badly needed, though the labour involved is considerable. I might add that, should the proportion of deaths due to predation prove to be high in any bird, it will be necessary to measure also the other mortality factors before the possible effects of predation on the population density of the species can be adequately assessed.

### *Evidence for limitation by food.*

Although predation may be important in some cases (notably in the gallinaceous birds with a 4-year or 10-year cycle), I would tentatively suggest that *food supply* may be the most usual factor regulating population density in birds. Circumstantial evidence that birds may be up against the food limit is reviewed in this section.

First, in agreement with Gause's principle (1934), closely related species of birds are normally isolated ecologically from each other. It is particularly significant that when two closely related species are not isolated by habitat but occur together in the same place, they normally show a marked difference in feeding methods or in size of beak, indicating that they take mainly different foods. This has been found to hold in passerine birds on oceanic islands (Lack, 1944, 1947a), in western Europe (Lack, 1944), and in tropical Africa (Moreau, 1948), also in European birds of prey (Lack, 1946a) and in species of *Phalacrocorax* (Lack, 1945). Such ecological divergence is presumably a result of natural selection, and its existence implies that the species concerned are potential food competitors, and hence that their numbers are limited by food. When food is temporarily super-abundant, and hence there is no competition, such ecological isolation often breaks down (Lack, 1946a; Moreau, 1948).

That the ecological isolation between related species is due to competition is corroborated by the fact that, where one species is absent, another often expands into its niche. This has happened in several cases among the Geospizinae on outlying islands of the Galapagos (Lack, 1947a, 1949a), and also in several passerine and near-passerine birds in the isolated montane forests of tropical Africa (Moreau, 1948). In tropical Africa, for instance, *Yungipicus* is typically a woodpecker of dry country, but in one isolated montane forest, Mbulu, the normal rain-forest woodpeckers are all absent, and here, but only here, *Yungipicus* is regular in rain-forest. Lack and Southern (1949) report parallel instances from the Canary Islands. In western Europe the Coal Tit (*Parus ater*) primarily frequents coniferous woods and the Blue Tit (*P. caeruleus*) broad-leaved woods. In the Canary Islands *P. ater* is absent, and here *P. caeruleus* is abundant in conifers, on one island, Palma, being nearly restricted to them. The subspecies of *P. caeruleus* in the Canary Islands, particularly *P. c. palmensis* on Palma, show remarkable convergence in appearance to *P. ater*, both in colour and beak, as illustrated in Fig. 7.

Profitable lines for further research on ecological isolation might be:

i) a study of ducks (Anatidae) at high latitudes, and of herons (Ardeidae) at low latitudes, as in both cases a large number of related species occur together in the same area;

ii) a comparison of the ecological niches of migratory passerine species in summer and winter, as in long-distance migrants the summer and winter quarters provide a rather different assemblage of related species which might be potential food competitors;

iii) a study of intergeneric competition. All the papers referred to above are concerned with competition between species in the same genus. There seem to be a number of cases where species in different genera apparently eat the same foods though species in the same genus are ecologically isolated; e. g. in Scandinavia, spruce (*Picea*) seeds are a major food item of Common Crossbill (*Loxia curvirostra*), Coal Tit (*Parus ater*) and Great Spotted Woodpecker (*Dryobates major*), but not of other species of *Loxia, Dryobates* or *Parus.*

A quite different indication that food supply may be limiting density is that, where the food density is higher, the bird density is also higher. Thus Jespersen (1924, 1929) showed that, in the North Atlantic, sea-birds are much more abundant in areas where plankton is common than where it is

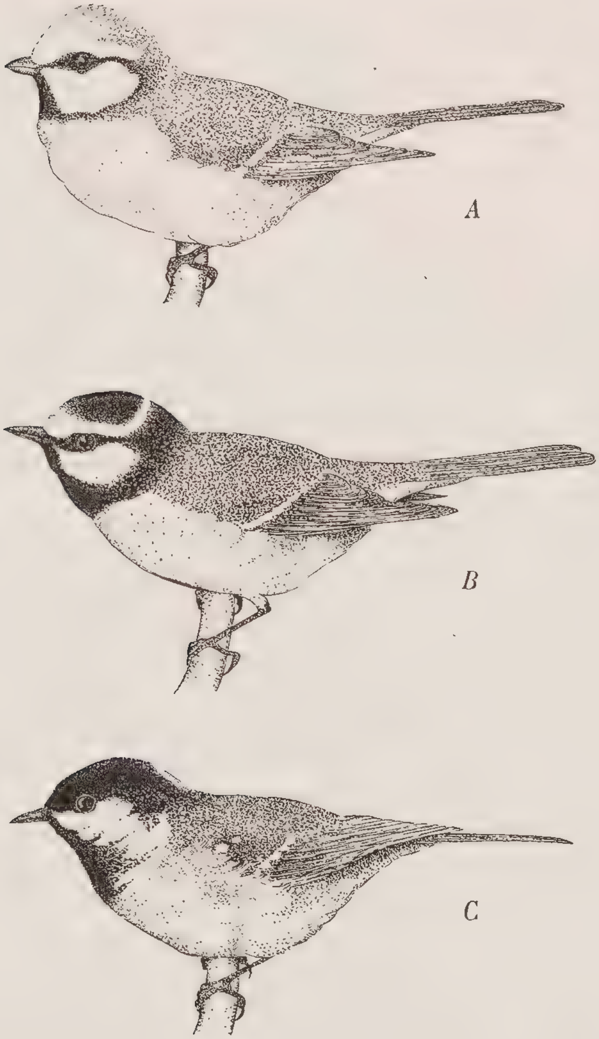


Fig. 7. *Parus c. caeruleus* (A), *P. c. palmensis* (B) and *P. a. ater* (C) showing resemblance of *P. c. palmensis* to *P. ater* (drawn by P. Sevenster).

scarce. Likewise in Finland, those woods which are the richest floristically also support the highest density of both insects and woodland birds (Palmgren, 1928, 1932; Kuusisto, 1941), while eutrophic lakes have a higher density of water birds than oligotrophic ones (Palmgren, 1936). Conversely, a bird may decrease markedly when its normal food has decreased, as in the case of the Brent Goose (*Branta bernicla*) and the eel-grass (*Zostera*)

(Cottam *et al.*, 1944), while the correlation by Reinikainen (1937) between the abundance of spruce cones and of the Crossbill (*Loxia curvirostra*) was mentioned earlier. Other such instances can be found in the literature, though in extremely few cases have actual measurements been made.

### *Food studies*

While there is such indirect evidence that food may limit bird density, extremely little direct quantitative evidence has yet been obtained. Indeed, even qualitative studies of the foods taken by a species throughout the year have rarely been made on an adequate scale, exceptions being the work of Pynnönen (1939, 1943) on the foods and feeding habits throughout the year of four species of woodpeckers in Finland, and a number of recent papers on the foods and food requirements of various American gallinaceous birds (mostly in *Journal of Wildlife Management*).

Fig. 8, taken from Baldwin and Kendeigh (1938), shows a bird's diurnal rhythm in feeding activity and weight throughout the day. Extensive measurements of this type are needed in the field under varying conditions of weather, season, habitat, region etc. The time of retiring to roost has been measured by Franz (1943), Brown (1946), Lehtonen (1947) and others, who find that passerine birds retire to roost later with respect to sunset in midwinter than in autumn, indicating that when the days are shortest, the birds need to collect food up to the last possible moment. The regular measurement of bird weights also throws valuable light on food requirements, in which connection may be mentioned the rise in weight in winter cold weather (Nice, 1938), and the rise in weight just prior to migration (Wolfson, 1945). Nice, Wolfson and others have worked with passerine birds, while Richdale (1947) has studied the seasonal changes in weight in penguins and petrels. In most other groups of birds, weight has not been studied on a quantitative or ecological basis.

The amount of food taken per day has occasionally been measured for young in the nest, as by Pynnönen, (1939, 1943), who enclosed the young in bags and weighed them at intervals, and also measured the parental feeding frequency with automatic recording. The amount of food taken per day by an adult bird in the wild is much harder to measure, and I know of only three records, these being given in the upper section of Table 17. Pynnönen (*loc. cit.*) could measure the food taken by a Great Spotted Woodpecker (*Dryobates major*), because it brought its pine cones to a few selected places for opening them. It is a pity that measurements could not have been made at the same time of the density of the woodpecker and the den-

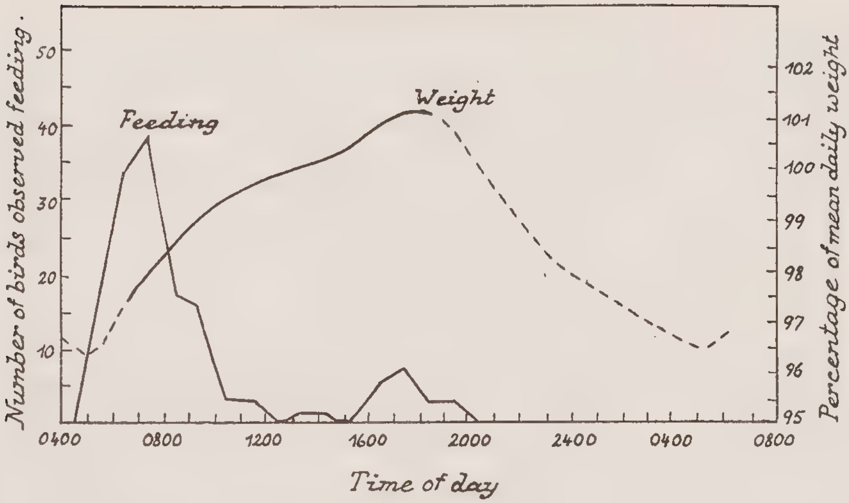


Fig. 8. Diurnal variations in feeding frequency and body weight (Baldwin and Kendeigh).

sity of pine cones. Fitch *et al.* (1946) found a wild Redtailed Hawk (*Buteo jamaicensis*) which was undisturbed by a human observer in the vicinity, and watched it for 21 days (not, however, successively), during which time the bird made only five kills. Gibb (in progress) could watch a Rock Pipit (*Anthus spinoletta petrosus*) feeding on the shore closely and continuously enough to establish that it took in one December day about 800–850 *Idotea* spp. and 1000-1200 very small *Littorina* (mainly *L. neritoides*), and scarcely anything else, spending $5\ ^{1}/_{2}$ hours searching for *Idotea*, $^{3}/_{4}$ hour searching for *Littorina* and 20 minutes drinking and preening by a freshwater stream. Further studies of these types are needed.

To determine whether food supply limits density, one must know not only the amount of food taken, but also both the amount available and the density of the bird. A start has been made with this difficult problem, existing knowledge being summarised in the second half of Table 17. Most of these studies suggest that birds take only a very small proportion of the available food. However, all except one of these studies relate to the breeding season. Birds normally breed at the season when their food is most abundant, when, indeed, it may be superabundant; hence conclusions based on the breeding season must not be applied to other times of the year. It seems reasonable to suppose that, at certain other seasons, notably in winter, birds take a much higher proportion of the available prey. It should be added that most of the estimates of food density used in the calculations

### Table 17. Food Studies.

### A. Amount taken by adult bird.

| | | |
|---|---|---|
| *Dryobates major* ..... | 12–13 pine cones (170 seeds, 0.8 gram) per hour | Pynnönen (1939) |
| *Buteo jamaicensis* .... | 5 kills in 21 days (100 grams per day) | Fitch *et al.* (1946) |
| *Anthus spinoletta* .... | c. 825 *Idotea* and c. 1 100 *Littorina* in one day | Gibb (in progress) |

### B. Percent prey taken.

(i) *In Breeding Season*

| Bird | Insect larvae | % taken | Reference |
|---|---|---|---|
| *Sturnus vulgaris* ........ | *Tipulid* | 0.8–1 % | Kluijver (1933) |
| *Compsothlypidae* etc. .... | *Archips fumiferana* | c. 4.3 % | Kendeigh (1947) |
| *Parus major* ........... | *Cheimatobia brumata* | < 1 % | Hartley (in press) |
| *Parus* spp. ............ | Lepidopterous and Tenthredinid | 0–37 % | Tinbergen (1949) |
| | Vertebrates | | |
| *Accipiter nisus* ......... | Passerines | 2.3–8.4 % | Tinbergen (1946) |
| *Asio flammeus* ......... | *Microtus agrestis* | < 1 % | Chitty (1938) |

(ii) *In Winter*

| | | | |
|---|---|---|---|
| *Asio flammeus* ......... | *Microtus pennsylvanicus* | 10.5 % | Banfield (1947) |

*Note:* Tinbergen (1949) found proportion of caterpillars taken by *Parus* spp. varied greatly with species, the highest being *Panolis flammea* 37 %, *Ellopia prosapiaria* 23 % and *Acantholyda nemoralis* 18 %. Likewise Tinbergen (1946) found *A. nisus* took of *Passer domesticus* 8.4 %, of *Fringilla coelebs* 2.6 %, of *Parus major* 5.7 % and of *P. ater* 2.3 %, in the month of May, these fractions representing respectively 79 %, 30 %, 44 % and 15 % of the estimated total mortality in this period.

summarised in Table 17 depend in part on assumptions; not every stage is based on direct measurement.

Outside the breeding season, the problem of measuring precisely the impact of a bird on its prey presents considerable technical difficulties. Probably the best method is to work with a marked population of the prey species in which the marks persist when the prey is taken by the bird. Then, the total population and the total mortality of the prey species can be measured by recapturing a sample of the population at intervals, and the impact of the bird can be assessed by measuring the total number of the prey that it takes, together with the proportion of marked individuals included. Two studies of this nature are now in progress at Oxford. H. N. Southern is working with the Tawny Owl (*Strix aluco*) and a marked population of the Bank

Vole (*Clethrionomys glareolus*) and Wood Mouse (*Apodemus sylvaticus*), whose metal tags can be recovered from the owl pellets. P. M. Sheppard, A. J. Cain and P. H. T. Hartley are working with the Song Thrush (*Turdus ericetorum*) and a marked population of the snail *Cepaea nemoralis*, the remains of which are left at the thrush anvils.

While the data in Table 17 show that a start has been made, it is not safe in the present state of ignorance to make even a rough guess at the probable proportion of its prey taken by a bird during the year, and the long-term effect of a bird on the numbers of its prey cannot be predicted at all. It may be added that, until these facts are known, so-called "economic ornithology" cannot even begin, and glib pronouncements that one species is "beneficial" and another "harmful" should be relegated to the domain of folk-lore. In particular, a passerine species must not be described as "beneficial" simply because it is known to eat harmful insects, nor should a hawk be considered "harmful" simply because it takes the passerine species in question. Before such pronouncements can be made, the bird's impact on its prey must be known in quantitative, not merely in qualitative, terms. Nor is this enough, for it is essential to measure likewise the other mortality factors affecting the prey. Moreover, all these measurements must be made over several years, to allow for annual variations.

The eventual aim is to measure quantitatively over a period of years the density of a bird and its prey, and the mortality factors affecting both. It will be difficult to find suitable species for such a study and the work will be extremely arduous, but this seems the only way of determining how bird numbers are regulated.

## Conclusion

This review ends rather in the air because, at this point, where the crux of the matter is reached, there is as yet no established basis of facts. It should, however, be remembered that, at the time of the last International Congress in 1938, a review such as the present would not have been possible at all. Hence while in 1950 the core of the problem remains to be elucidated, in 1938 the existence of the problem was hardly realised. In the last twelve years great progress has been made in regard to long-term censuses, breeding seasons, clutch-size, nestling mortality, adult mortality and average age, while irruptions and cycles are rather better understood, and a start has been made with predation and food studies. Hence much has been achieved, and it is stimulating to have been asked to review a subject in which knowledge has been advancing so rapidly.

*Discussion:*

J. Harrison: In considering the mortality of birds in connection with the subject of population dynamics, the transmission of disease, particularly tuberculosis, or an acid fast disease caused by a morphologically very similar organism, is of importance.

Several instances of this have been reported both in species which would be the prey, and also in birds of the predator category.

Harrison (1946) recorded four species, viz. Pheasant (*Phasianus colchicus, Larus ridibundus, Sturnus vulgaris, Asio flammeus*), quoting also Mitchell and Duthie (1929) as recording 15 % of 40 Crows as tuberculous. In the same communication Harrison mentions the following as having been subject to this disease, *Columba palumbus, Fringilla coelebs, Passer domesticus,* and *Vanellus vanellus.* In predators Kalter *et alia* (1930 recorded the disease in the Eastern Sparrow-Hawk, and Rooke (1946) noted it in the Barn-Owl (*Tyto alba*). Amongst the passerines it has been found in the Blackbird (Turdus merula) by Hare (1931–32), while I have recently recorded this disease in an adult male of the European Sparrow-Hawk (*Accipiter nisus*) (1948).

The disease is transmitted through the digestive tract, and the above published instances in species both of the preyed upon and predator class indicates a factor in mortality dynamics offering an interesting field for research, and one having possibly some bearing upon the subject of Dr David Lack's interesting communication.

HARE, T. 1931–32. Proc. Roy. Soc. Med., XXV, 1500.
HARRISON, J. G. 1946. St Thos. Hosp. Gaz., XLIV, 202.
HARRISON, J. M. 1948. Jnl. Path. & Bact. LX, 583–586.
KALTER, L. B., FEDERICHI, H., & INMAN, O. L. 1933. Ohio Jnl. Sci. XXXIII, 451.
MITCHELL, C. A. & DUTHIE, R. C. 1929. Amer. Rev. Tuberc., XIX, 134.
ROOKE, K. B. 1946. Ohio Jnl. Sci. LXXXVIII, 394

T. Lampio: In connection with the four year and ten year periodicity, which were mentioned here by Dr Lack, I will mention the recent investigations of Dr Siivonen. According to them the real periodicity seems to be—not four years—but 3–4, and that the ten year periodicity and the shorter one in fact are the same phenomenon.

Then there seems to be a special group of animals living in coniferous forests. The squirrel (*Sciurus vulgaris*) and also some birds, as *Pinicola* and *Loxia,* belong to this group, which has a five year peridiocity.

D. Lack: I think Dr Siivonen's suggestion that the 3–4 year lemming cycle and the 10 year cycle are linked, is not proven, but is interesting and should be further investigated.

I disagree with Mr Lampio about *Pinicola* and *Loxia.* I think they show irregular not regular invasions and that the interval between succesive invasions also varies markedly in different places. I do not think these species should be classified with the cycles of gallinaceous birds, as is sometimes done.

D. E. Sergeant: Do you consider it possible that the cycle of the lemmings and of the gallinaceous birds in the same areas may be linked directly by disease?

D. Lack: I think it unlikely that disease should spread from the rodents to the gallinaceous birds.

American work suggests that disease occurs among the rodents and sometimes among the game-birds in a crash, but it may be a different disease on different occasions, often a deficiency disease, and the bird diseases have not, so far as I know, been recorded among the rodents, and conversely.

## References

Austin, O. L., 1942. The life span of the Common Tern. (*Sterna hirundo*). Bird Band. 13: 159–176. (See also D. Lack in Ibis 1943, p. 365).

Baldwin, S. P. and Kendeigh, S. C., 1938. Variations in the weight of birds. Auk 55: 416–467.

Banfield, A. W. F., 1947. A study of the winter feeding habits of the Short-eared Owl (*Asio flammeus*) in the Toronto region. Canad. J. Research 25 D: 45–65.

Berndt, R., 1949. Zwölf Jahre Kontrolle des Höhlenbrüterbestandes eines nordwestsächsischen Parkes. Beiträge zur Vogelkunde ed. G. Creutz: 1–20.

Bourlière, F., 1947. Quelques remarques sur la longevité dans la nature du Freux et du Heron cendré. L'Oiseau 17: 178–181.

Braestrup, F. W., 1941. A study on the arctic fox in Greenland. Medd. Grønland 131: 1–101.

Brown, F. J., 1946. A Cheshire Starling roost, 1944–5. J. Anim. Ecol. 15: 75–81.

Bump, G., Darrow, R. W., Edminster, F. C., Crissey, W. F. 1947. The Ruffed Grouse: Life History, Propagation, Management.

Chitty, D., 1938. A laboratory study of pellet formation in the Short-eared Owl (*Asio flammeus*). Proc. Zool. Soc. 108 A: 267–287.

Chitty, D. and Elton, C. 1940. The Snowshoe Rabbit enquiry, 1938–39. Canad. Field Nat. 54: 117–124.

Chitty, H., 1943. Canadian arctic wild life enquiry, 1941–42. J. Anim. Ecol. 12: 163–172.

Chitty, H. and D., 1945. Canadian arctic wild life enquiry, 1942–43. J. Anim. Ecol. 14: 37–45.

Clarke, C. H. D., 1936. Fluctuations in Ruffed Grouse, *Bonasa umbellus* (Linné) with special reference to Ontario. Univ. Toronto Studies. Biol. Ser. 41: 1–118.

Comeau, N. A., 1909. Life and Sport on the North Shore of the Lower St. Lawrence and Gulf, pp. 284–295.

Cottam, C., Lynch, J. J., Nelson, A. L., 1944. Food habits and management of American Sea Brant. J. Wildlife Manag. 8: 36–56.

Criddle, N., 1930. Some natural factors governing the fluctuations of grouse in Manitoba. Canad. Field. Nat. 44: 77–80.

Edminster, F. C., 1947. The Ruffed Grouse: its Life Story, Ecology and Management.

Einarsen, A. S., 1945. Some factors affecting Ring-necked Pheasant population density. Murrelet 26: 39–44.

Elton, C., 1942. Voles, Mice and Lemmings—Problems in Population Dynamics.

Elton, C. and Nicholson, M., 1942. The ten-year cycle in numbers of the Lynx in Canada. J. Anim. Ecol. 11: 215–244.

Emlen, J. T., 1940. Sex and age ratios in survival of the California Quail. J. Wildlife Manag. 4: 92–99.

Errington, P. L., 1945. Some contributions of a fifteen-year local study of the Northern Bobwhite to a knowledge of population phenomena. Ecol. Monog. 15: 1–34.

Farner, D. S., 1949. Age groups and longevity in the American Robin: comments, further discussion and certain revisions. Wilson Bull. 61: 68–81.

Fitch, H. S., Swenson, F., Tillotson, D. F., 1946. Behaviour and food habits of the Red-tailed Hawk. Condor 48: 205–237.

Franz, J., 1943. Ueber Ernährung und Tagesrhythmus einiger Vögel im arktischen Winter. J. f. Orn. 91: 154–165.

Gause, G. F., 1934. The Struggle for Existence.

Gibb, J. A., 1950. The breeding biology of the Great and Blue Titmice. Ibis 92: 507–539.

Goethe, F., 1939. Die Vogelinsel Mellum. Abh. Geb. Vogelk. No. 4.

Grange, W. B., 1948. Wisconsin Grouse Problems. (Wisconsin Conservation Dept.)

Green, R. G., Larson, C. L., and Bell, J. F., 1939. Shock disease as the cause of the periodic decimation of the snowshoe hare. Amer. J. Hyg. 30B: 83–102.

Griscom, L., 1937. A monographic study of the Red Crossbill. Proc. Boston Soc. Nat. Hit. 41: 77–210.

Haartman, L. v., 1949. Der Trauerfliegenschnäpper. 1. Ortstreue und Rassenbildung. Act. Zool. Fenn. 56, pp. 104.

Höhn, E. O., 1948. Mortality of adult and young Mallards. Brit. Birds 41: 233–235.

Hornberger, F., 1943. Einige Ergebnisse zehnjähriger Planarbeit im „Storchforschungskreis Insterburg“ der Vogelwarte Rossitten. J. f. Orn. 91: 341–355.

Jespersen, P., 1924, 1929. The frequency of birds over the high Atlantic Ocean. Nature 114: 281–283, and Verh. VI. Int. Orn. Kongr. 1926, pp. 163–172.

Johnsen, S., 1929. Rovdyr- og rovfuglstatistikken i Norge. Bergens Museums Årbok. 1929. 2: 5–118.

Kalela, O., 1949. Changes in geographic ranges in the avifauna of northern and central Europe in relation to recent changes in climate. Bird Band. 20: 77–103.

Kendeigh, S. C., 1947. Bird population studies in the coniferous forest biome during a Spruce Budworm outbreak. Dept. Lands and Forests, Ontario. Biol. Bull. No. 1.

Klomp, H., 1946. Verslag van het Kievitenringstation „Reeuwijk" over de jaren 1943–1945 en gegevens over de trek van de Kievit. Limosa 19: 76–117.

Kluijver, H. N., 1933. Bijdrage tot de biologie en de ecologie van den Spreeuw (*Sturnus vulgaris vulgaris* L.) gerurende zijn voortplantingstijd. Med. Plantenziektenkundigen Dienst Wageningen no. 69, pp. 145.

Kluijver, H. N., 1935. Waarnemingen over de levenswijze van den Spreeuw (*Sturnus v. vulgaris* L.) met behulp van geringde individuen. Ardea 24: 133–166.

Kraak, W. K., Rinkel, G. L., and Hoogerheide, J., 1940. Oecologische bewerking van de Europese ringgegevens van de Kievit (*Vanellus vanellus* (L)). Ardea 29: 151–175.

Kuusisto, P., 1941. Studien über die Ökologie und Tagesrhythmik von *Phylloscopus trochilus acredula* (L.) Act. Zool. Fenn. 31.

Lack, D., 1943a. The Life of the Robin, pp. 127–138.

Lack, D., 1943b. The age of some more British birds. Brit. Birds 36: 193–221.

—— 1944. Ecological aspects of species-formation in passerine birds. Ibis 1944: 260–286.

—— 1945. Ecology of closely related species with special reference to Cormorant and Shag. J. Anim. Ecol. 14: 12–16.

—— 1946a. Competition for food by birds of prey. J. Anim. Ecol. 15: 123–129.

—— 1946b. Do juvenile birds survive less well than adults? Brit. Birds 39: 258–264.

—— 1947a. Darwin's Finches.

—— 1947b. The significance of clutch-size in the Partridge (*Perdix perdix*). J. Anim. Ecol. 16: 19–25.

—— 1947–8. The significance of clutch-size. Ibis 89: 302–352; 90: 25–45.

—— 1948a. Natural selection and family size in the Starling. Evolution 2: 95–110.

—— 1948b. Notes on the ecology of the Robin. Ibis 90: 252–279.

—— 1949a. The significance of ecological isolation. Genetics, Paleontology and Evolution (ed. Jepsen *et al*) 299–308.

—— 1949b. Family size in certain Thrushes (*Turdidae*). Evolution 3: 57–66.

—— 1949c. The apparent survival-rate of ringed Herons. Brit. Birds 42: 74–79.

—— 1949d. Vital statistics from ringed Swallows. Brit. Birds 42: 147–150.

Lack, D., and Arn, H., 1947. Die Bedeutung der Gelegegrösse beim Alpensegler. Ornith. Beob. 44: 188–210.

Lack, D. and Schifferli, A., 1948. Die Lebensdauer des Stares. Ornith. Beob. 45: 107–114.

Lack, D. and Silva, E. T., 1949. The weight of nestling Robins. Ibis 91: 64–78.

Lack, D. and Southern, H. N., 1949. Birds on Tenerife. Ibis 91: 607–626.

Laven, H., 1940. Beiträge zur Biologie des Sandregenpfeifers (*Charadrius hiaticula* L.). J. f. Orn. 88. 183–287.

Lehtonen, L., 1947. Zur Winterbiologie der Kohlmeise, *Parus m. major* L. Orn. Fenn. 24: 32–47.

Leiper, R. T., 1911. On the development and bionomics of *Trichostrongylus pergracilis*, in *The Grouse in Health and Disease* 1: 218–234.

Leopold, A. and Ball, J. N., 1931. British and American grouse cycles. Canad. Field Nat. 45: 162–167.

Lotka, A. J., 1925. Elements of Physical Biology.

MacLulich, D. A., 1937. Fluctuations in the numbers of the Varying Hare (*Lepus americanus*). Univ. Toronto Studies Biol. Ser. 43. 1–136.

McIlhenny, E. A., 1940. Sex ratio in wild birds. Auk 57: 85–93.

Magnusson, M. and Svärdson, G., 1948. Livslängd hos tornsvalor (*Micropus apus* L.). Vår Fågelvärld 7: 129–144.

Moran, P. A. P., 1949. The statistical analysis of the sunspot and lynx cycles. J. Anim. Ecol. 18: 115–116.

Moreau, R. E., 1947. Relations between number in brood, feeding-rate and nestling period in nine species of birds in Tanganyika Territory. J. Anim. Ecol. 16: 205–209.

—— 1948. Ecological isolation in a rich tropical avifauna. J. Anim. Ecol. 17: 113–126.

Nice, M. M., 1937. Studies in the life history of the Song Sparrow, Vol. 1. Trans. Linn. Soc. New York. 4.

—— 1938. The biological significance of bird weights. Bird Band. 9: 1–11.

Nicholson, A. J., 1933. The balance of animal populations. J. Anim. Ecol. 2: 132–178.

Nicholson, E. M., 1935–1938, and Alexander, W. B., 1940–1950. An index of Heron population. Brit. Birds vols. 28 onwards.

Palmgren, P., 1928. Zur Synthese pflanzen- und tierökologischer Untersuchungen. Act. Zool. Fenn. 6.

Palmgren, P., 1932. Zur Biologie von *Regulus r. regulus* (L) und *Parus atricapillus borealis* Selys. Eine vergleichend. u. ökologische Untersuchung. Act. Zool. Fenn. 14: 1–113.

—— 1936. Über die Vogelfauna der Binnengewässern Ålands. Act. Zool. Fenn. 17.

Paynter, R. A. (1947). The fate of banded Kent Island Herring Gulls. Bird Banding 18: 156–170.

—— 1949. Clutch-size and the egg and chick mortality of Kent Island Herring Gulls. Ecology 30: 146–166.

Plattner, J. and Sutter, E., 1946–7. Ergebnisse der Meisen- und Kleiberberingung in der Schweiz. (1929–1941.) Orn. Beob. 43: 156–188; 44: 1–35.

Pynnönen, A., 1939, 1943. Beiträge zur Kenntnis der Biologie finnischer Spechte. Ann. Soc. Zool.-Bot.-Fenn. Vanamo. 7, No. 2: 9 No 4.

Reinikainen, A., 1937. The irregular migrations of the Crossbill, *Loxia c. curvirostra*, and their relation to the cone-crop of the conifers. Orn. Fenn. 14: 55–64.

Richdale, L. E., 1947. Seasonal fluctuations in weights of penguins and petrels. Wilson Bull. 59: 160–171.

Ruiter, C. J. S., 1941. Waarnemingen omtrent de levenswijze van de Gekraagde Roodstaart, *Phoenicurus ph. phoenicurus* (L). Ardea 30: 175–214.

Schenk, J., 1929. Die Brutinvasion des Rosenstares in Ungarn im Jahre 1925. Verh. VI. Int. Orn. Kongr. 1926, pp. 250–264.

Schorger, A. W., 1947. The Ruffed Grouse in early Wisconsin. Trans. Wisconsin Acad. Ser. 37: 35–90.

Schüz, E., 1940. Bewegungen im Bestand des Weissen Storches seit 1934. Orn. Monatsb. 48: 1–14.

Serebrennikov, M. K., 1931. Der Rosenstar (*Pastor roseus* L.), seine Lebensweise und ökonomische Bedeutung in Uzbekistan (Turkestan). J. f. Orn. 79: 29–56.

Serventy, D. L. and Whittell, H. M., 1948. A Handbook of the Birds of Western Australia.

Shelford, V. E., 1945. The relation of Snowy Owl migration to the abundance of the Collared Lemming. Auk 62: 592–6.

Siivonen, L., 1941. Über die Kausalzusammenhänge der Wanderungen beim Seidenschwanz, *Bombycilla g. garrulus* (L). Ann. Zool. Soc. Zool.-Bot. Fenn. Vanamo 8, no. 6.

Skutch, A. F., 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430–455. Comments by D. Lack: 455–458.

Smith, H. S., 1935. The role of biotic factors in the determination of population densities. J. Econ. Entom. 28: 873–898.

Speirs, J. M., 1939. Fluctuations in numbers of birds in the Toronto region. Auk 56: 411–419.

Tinbergen, L., 1946. De Sperwer als roofvijand van Zangvogels. Ardea 34: 1–213.

—— 1949. Bosvogels en insecten. Nederl. Boschbouw Tijds. 4: 91–105.

Tischler, F., 1941. Die Vögel Ostpreussens vol. I.

Varley, G. C., 1947. The natural control of population balance in the Knapweed Gall-fly (*Urophora jaceana*). J. Anim. Ecol. 16: 139–187.

Volterra, V., 1928. Variations and fluctuations of the number of individuals in animal species living together. Appendix to Chapman, R. N. (1931) Animal Ecology, with especial reference to insects, pp. 409–448.

Warga, K., 1935–38. Die *Bombycilla g. garrulus* Invasion in den Jahren 1931/32 und 1932/33, und die Ergebnisse der Beringungsversuche. Aquila 42–45: 490–528.

Witherby, H. F. et al., 1938. The Handbook of British Birds. Vol. I, II.

Wolfson, A., 1945. The role of the pituitary, fat deposition, and body weight in bird migration. Condor 47: 95–127.

# The changes in the distribution of the fulmar (Fulmarus glacialis)

*James Fisher*

*Ashton, England*

The northern fulmar, *Fulmarus glacialis,* lives in the North Pacific, North Atlantic and North Polar Basin. It is closely related to *Fulmarus glacialoides* which breeds round the Antarctic continent and on some of its neighbouring islands. Indeed, as K. H. Voous has recently suggested (1949), *F. glacialis* is probably descended from *F. glacialoides.* The two species are remarkably similar, differing principally in the shape and length of their bills.

The northern fulmar has two main populations. *F. g. rodgersii* breeds in the North Pacific in the Kuriles, Commander Is., various of the Aleutians, the Pribilof Is. and on St. Matthew and Hall Is. It probably breeds in Chukotskii Land, and may also breed on St. Lawrence I., though this is unlikely; and has been alleged to breed on Kamchatka, on Wrangel and Herald Is., and on Prince Albert Land in the Canadian Arctic Archipelago. I cannot trace the original observations upon which these allegations are based, save that of Herald Island, which by no means constitutes proof of breeding. *F. g. glacialis* breeds at at least three, and possibly several other places round Baffin Island, at one or two places on Devon Island, on an islet south of Ellesmere Island, on nine or ten islets and promontories belonging to West Greenland, in East Greenland at three places in the north-east and one island off Scoresby Sound, in at least thirty-four places in Spitsbergen, at least nine in Franz Josef Land, at one or two in north Novaya Zemlya, probably not on Lonely Island as has been alleged, on Bear Island, on Jan Mayen, in Iceland, Faeroe, Norway and the British Isles. *F. glacialis* (and probably also *F. glacialoides*) is polymorphic; its Pacific and Atlantic populations each contain forms ranging from dusky blue-grey to light with white heads and under-parts. The extremes appear to be further apart in the Pacific population. The intermediates are often difficult to assign in the field to the 'dark' side or the 'light' side. Fig. 1 represents the situation at the breeding-colonies as it is now known.

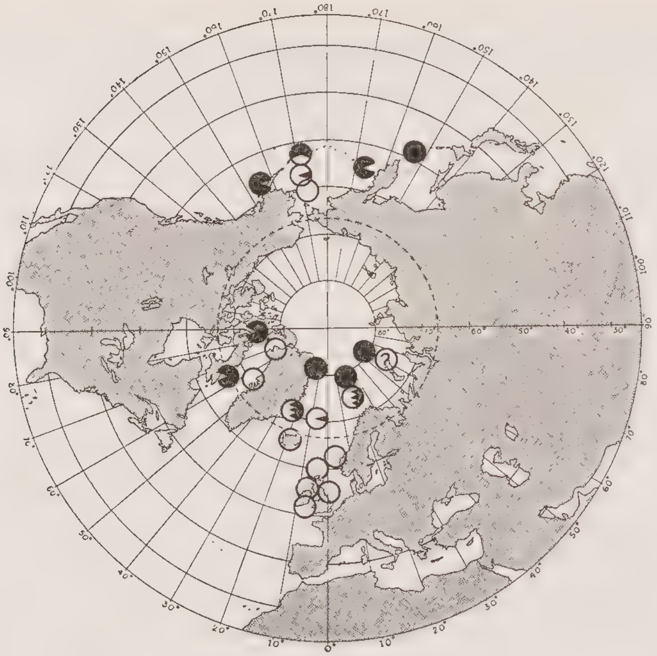


Fig. 1. Breeding distribution of the fulmar. The amount of black occupying each circle indicates the approximate proportion of dark coloured fulmars in the breeding population.

For two hundred years the populaton of the light-coloured fulmars in the eastern Atlantic has been increasing: the increase has now become a phenomenon which has no parallel in the world of birds and few in that of vertebrates.

The colonies in the Iceland—Britain area in the middle of the eighteenth century appear to have consisted of a colony on St. Kilda, the westernmost island-group of Scotland, which appeared to be of much the same size as it has now when it was first described by Martin Martin in 1697. In Iceland a colony was described on Grímsey, the northernmost island, by Jón Guðmundsson laerði (the learned) in about 1640; there may in the seventeenth century have been another on the stack of Kolbeinsey further north, which is now eroded away. St. Kilda and Grímsey had the only known certain fulmar colonies in this area until the seventeenth century. Up to 1713 there was almost certainly no fulmar colony in the Westmann Islands, south of Iceland. In about 1753 the fulmar was found nesting here, and at the same time on Eldey, a stack off the south-west. There is no evidence of any other fulmar colonies in Iceland during the eighteenth century.

In 1821 what was to become a rapid spread of the fulmar as a breeding species in south Iceland began at a coastal mountain on the mainland nearest the Westmanns known as Höfðabrekkuháls. In the same year fulmars also colonised two cliffs in south-west Iceland not far from Eldey; from here they spread east and north. In 1821, too, fulmars were found breeding at Látrabjarg in the north-west peninsula, which now has fulmar colonies on nearly all its prominent capes. The colonisation of east Iceland did not start until about 1894, and that of north Iceland not until about 1900; but Iceland is now surrounded by fulmar colonies, of which, with the most generous help of Dr Finnur Guðmundsson, Dr Pálmi Hannesson, Þorsteinn Einarsson and many other Icelanders, whom I met on my visit to Iceland in 1949, I can distinguish no less than 155 (1949). Some of these have been large for many years, particularly the Westmann Islands and the colonies in the Mýrdal area in south Iceland; from each of these groups over twenty thousand young were taken in some years at the end of the last, and in the present, century. The colony on Eldey has, incidentally, remained very small, as have some other early colonies. The Grímsey colony has produced over five thousand young a year; but here and at the Westmanns the fulmars are now decreasing—the only places where such seems to be the case. Elsewhere in Iceland the increase continues. No fulmar has been legally taken for food in Iceland since 1940.

It seems clear that the fulmar nested for the first time on Suðuroy, the southernmost island of Faeroe, some time between 1816 and 1839. It is reasonable to suppose that the birds came from the Westmann Isles. From Suðuroy the fulmars have colonised every island of Faeroe, large and small, from the south, mainly along the great cliffs of the west coast, then along the north coast to the north-easterly islands. Every important island was colonised by 1900, and I can recognise only twenty-two present colonies simply because breeding is so continuous round the cliffs that there is seldom an English mile of space between nests, which I take to assign such nests to different colonies. The take of young fulmars in Faeroe has been very high in the present century (it was stopped because of the psittacosis in 1936); by the early nineteen-thirties no less than eighty thousand young were being killed annually. This is one-third as much again as the highest take of young (59 830 in 1900) recorded for the whole of Iceland; nevertheless Iceland has had, and still I am sure has, a very much higher fulmar population than Faeroe.

The coming of the fulmar to Britain, and its subsequent spread round our coasts to 1939, was fully described by Fisher and Waterston (1941). Since 1939 much further increase has taken place, which I can illustrate

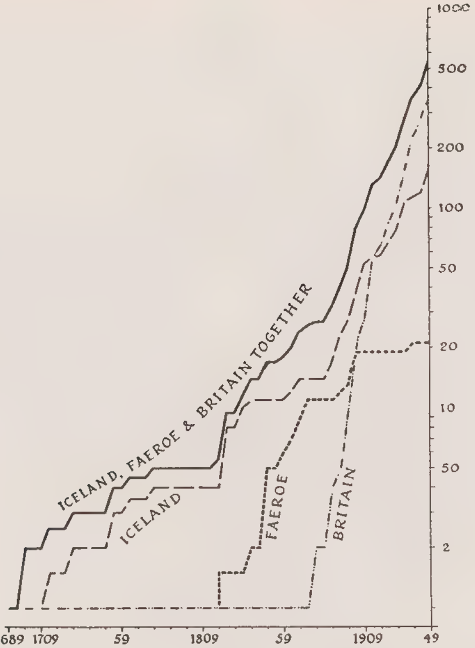


Fig. 2. The number of known breeding colonies of the fulmar in Iceland, Faeroe and Britain, 1689–1949 (logarithmic ordinate).

best by saying that in 1939 I now know there were about 273 breeding-colonies, and 132 cliffs where fulmars were prospecting without breeding; while in 1949 I had information of 365 breeding-colonies, and 212 prospecting colonies. Fulmars are now arriving at thirty-three new cliffs in Britain every year, on the average for the last five years.

Figure 2 shows the increase in the number of colonies in Iceland, Britain and Faeroe. It can be seen—particularly as the figure is on an 'arithlog' plot—that the number of colonies have been increasing by geometrical progression until the present day. I should mention that fulmars started to breed on Rundø in west Norway near the latitude of Shetland in 1924, having prospected since 1920, presumably from Shetland where the fulmar was by then abundant. The population in 1947 was three to four hundred nests and the fulmars have not yet, as far as I know, spread to other parts of Norway.

By collecting the British colonies into logarithmic categories (under 10 eggs laid, under 100, under 1000, etc.) and from what I have discovered by direct count and estimation of the nests at all the larger colonies (I have myself seen, often several times, all the colonies in Britain with over a hund-

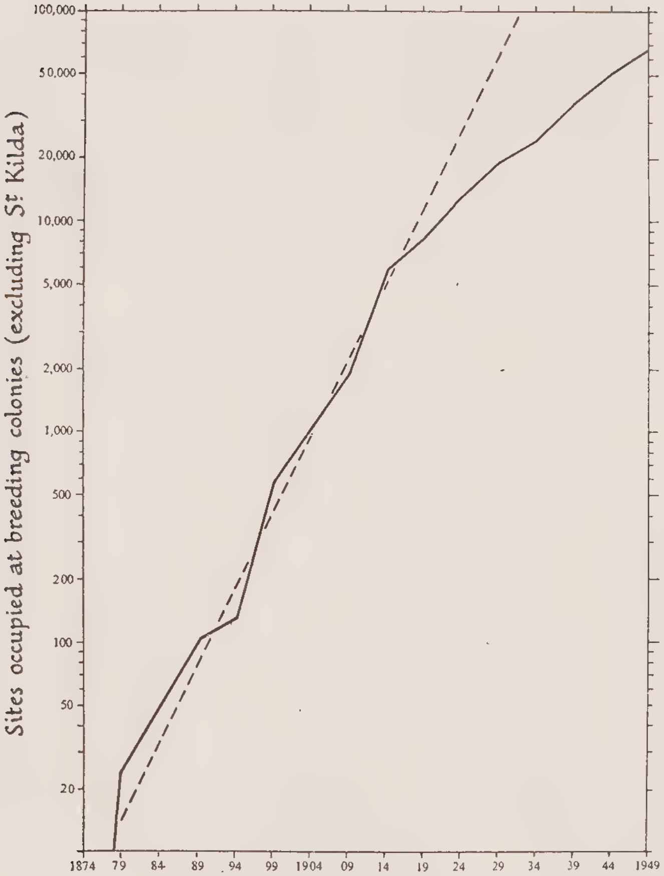


Fig. 3. The approximate number of nest sites occupied by fulmars in Britain apart from St. Kilda, 1874–1949 (logarithmic ordinate). The dotted line represents that increase which would have taken place had fulmars been immortal and perpetually fertile and had a 50: 50 sex-ratio, in the absence of colonisation of Britain from the outside. It will be noted that the actual increase until about 1914 approximated to this theoretical increase, which is proof of continuous colonisation from the outside.

red nests, and over half the rest, except for Ireland) I have arrived at figures for the approximate population of occupied nest-sites in the British Isles every fifth year since the spread started. The device which I have used to arrive at these figures had a crude form in my earlier paper with Waterston, has been improved (I hope) and will be fully described in a forthcoming work. I meanwhile offer the following table and figure as a *first approximation* to the trend of the fulmar's population in Britain, excluding that of the great ancient colony at St. Kilda, which as far as can be seen remained of the order of twenty to thirty thousand nests until 1939; in 1949 I found a surprising increase to about forty thousand nests.

A glance at Fig. 3 will show that the fulmar has increased, in Britain geometrically. The *annual* increase between 1878 and 1914 was at the extraordinary rate of about 18 %. After 1914 it fell to 7 % but has consistently remained at this rate. Up to 1914 this is proof of, and after 1914 is highly suggestive of, continuous colonisation from outside.

**Table 1. The number of known fulmar breeding-colonies in Iceland, Faeroe and Britain, 1689 to 1949.**

| Year | Iceland | Faeroe | Britain | Norway | Total |
|---|---|---|---|---|---|
| 1689 | 1 | | | | 1 |
| 1694 | 1 | | | | 1 |
| 1699 | 1 | | 1 | | 2 |
| 1704 | 1 | | 1 | | 2 |
| 1709 | 1 | | 1 | | 2 |
| 1714 | 1 or 2 | | 1 | | 2—3 |
| 1719 | 1 or 2 | | 1 | | 2—3 |
| 1724 | 1 or 2 | | 1 | | 2—3 |
| 1729 | 1, 2 or 3 | | 1 | | 2—4 |
| 1734 | 1, 2 or 3 | | 1 | | 2—4 |
| 1739 | 1, 2 or 3 | | 1 | | 2—4 |
| 1744 | 1, 2 or 3 | | 1 | | 2—4 |
| 1749 | 1, 2 or 3 | | 1 | | 2—4 |
| 1754 | 2, 3 or 4 | | 1 | | 3—5 |
| 1759 | 2, 3 or 4 | | 1 | | 3—5 |
| 1764 | 3 or 4 | | 1 | | 4—5 |
| 1769 | 3 or 4 | | 1 | | 4—5 |
| 1774 | 3 or 4 | | 1 | | 4—5 |
| 1779 | 4 | | 1 | | 5 |
| 1784 | 4 | | 1 | | 5 |
| 1789 | 4 | | 1 | | 5 |
| 1794 | 4 | | 1 | | 5 |
| 1799 | 4 | | 1 | | 5 |
| 1804 | 4 | | 1 | | 5 |
| 1809 | 4 | | 1 | | 5 |
| 1814 | 4 | | 1 | | 5 |
| 1819 | 4 | 0 or 1 | 1 | | 5—6 |
| 1824 | 8 | 0 or 1 | 1 | | 9—10 |
| 1829 | 8 | 0 or 1 | 1 | | 9—10 |
| 1834 | 10 | 0 or 1 | 1 | | 11—12 |
| 1839 | 11 | 1 | 1 | | 14 |

| Year | Iceland | Faeroe | Britain | Norway | Total |
|---|---|---|---|---|---|
| 1844 | 11 | 1 | 1 | | 14 |
| 1849 | 11 | 5 | 1 | | 17 |
| 1854 | 11 | 5 | 1 | | 17 |
| 1859 | 11 | 6 | 1 | | 18 |
| 1864 | 12 | 7 | 1 | | 20 |
| 1869 | 14 | 9 | 1 | | 24 |
| 1874 | 14 | 11 | 1 | | 26 |
| 1879 | 14 | 11 | 2 | | 27 |
| 1884 | 14 | 11 | 2 | | 27 |
| 1889 | 17 | 11 | 4 | | 32 |
| 1894 | 23 | 12 | 5 | | 40 |
| 1899 | 28 | 13 | 10 | | 51 |
| 1904 | 39 | 19 | 21 | | 79 |
| 1909 | 52 | 19 | 28 | | 99 |
| 1914 | 56 | 19 | 56 | | 131 |
| 1919 | 58 | 19 | 65 | | 142 |
| 1924 | 67 | 19 | 84 | 1 | 171 |
| 1929 | 79 | 19 | 104 | 1 | 203 |
| 1934 | 108 | 19 | 151 | 1 | 279 |
| 1939 | 112 | 21 | 227 | 1 | 361 |
| 1944 | 119 | 21 | 273 | 1 | 414 |
| 1949 | 155 | 21 | 365 | 1 | 542 |

Table 2. Approximate number of nest-sites occupied in Britain, excluding St. Kilda.

| | |
|---|---|
| 1878 | 12 |
| 1879 | 24 |
| 1884 | 50 |
| 1889 | 100 |
| 1894 | 130 + |
| 1899 | 580 |
| 1904 | 1 100 |
| 1909 | 2 000 |
| 1914 | 5 800 |
| 1919 | 8 500 |
| 1924 | 13 000 |
| 1929 | 19 000 |
| 1934 | 24 000 |
| 1939 | 36 000 |
| 1944 | 51 000 |
| 1949 | 68 000 |

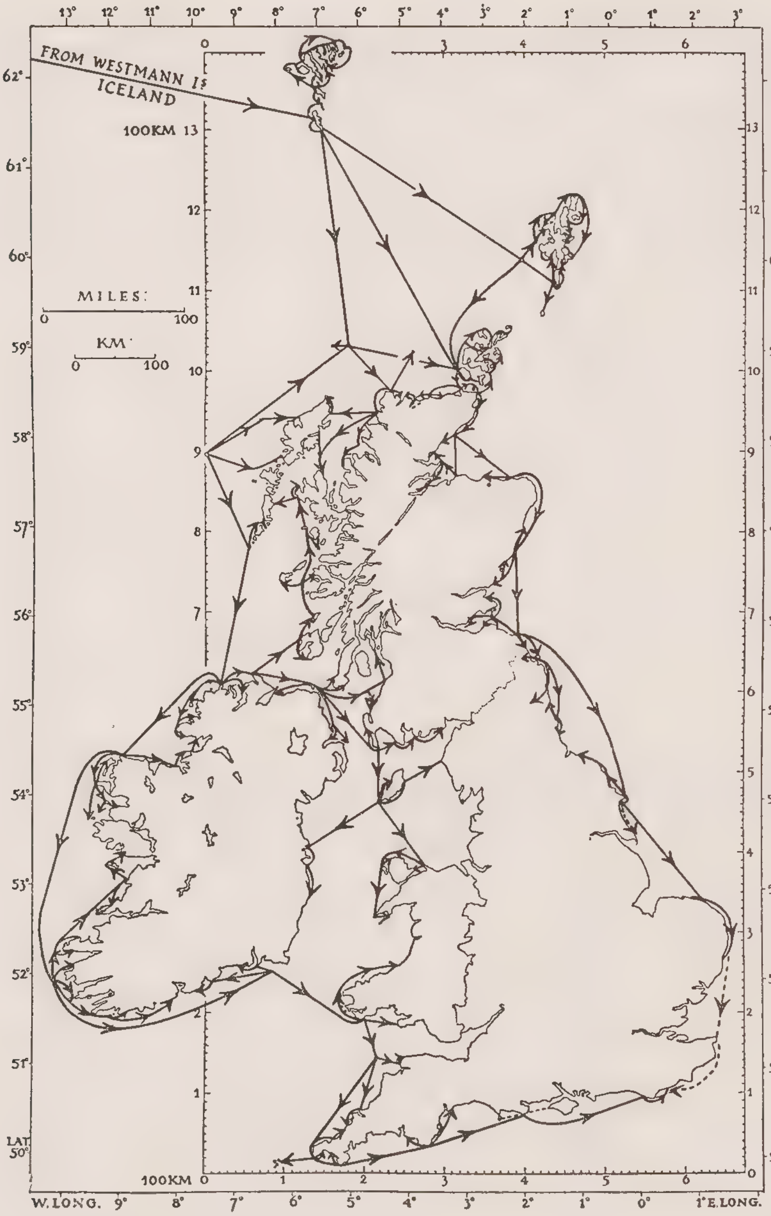


Fig. 4. The directions of spread of the fulmar to its present breeding-quarters in the British Isles.

The actual details of the spread are best shown by a system of arrows, each arrow pointing to a colony originating from the nearest colony to be previously prospected. The result is shown on Fig. 4.

It must be stressed, however, that the population is still chiefly concentrated in the north, though the British Isles are now almost completely surrounded by a network of small colonies, and busy prospecting fulmars are now gliding past almost anything that passes for a cliff, even near the watering-places of southern England, like Margate and Hastings. Fig. 5 shows the approximate distribution of population in a series of maps showing the situation in every tenth year up to 1949.

So the fulmar has increased, in the area Iceland—Britain, by geometrical progression (though not always at the same rate of geometrical progression) for two hundred years. What is the reason for this?

We can shortly dismiss climate. Since 1750 the climate of the region has fluctuated very much. In the present century it has ameliorated. The period of amelioration has coincided with the fulmar's most southward advance; if it had any effect on the fulmar we could expect it to drive the bird north, as it has driven other species; not south.

We have dismissed a change in human exploitation in our previous paper. At St. Kilda human exploitation, which removed about ten thousand young fulmars (half the annual hatch) a year consistently up to 1921, had nothing to do with the spread, as Fisher and Waterston have already shown. In Iceland and Faeroe the great fulmar-fowling was a consequence of, and not a cause of or, it appears, a hindrance to, the continued spread.

Has the fulmar suddenly changed its habits, through some inward change; has it changed its tolerance to the environment? Has it, for instance, begun to breed annually, instead of intermittently, as Wynne-Edwards and others suggest it does? I must say that I do not find the evidence for the intermittent breeding of the fulmar very strong, and I am certain it can not have occurred among healthy birds in the Iceland—Britain population. It *may* occur among the Davis Strait-Baffin Bay fulmars, which appear to have static populations. Further research is needed. Meanwhile I cannot believe that a revolution of this sort can have taken place other than as a response to a substantial, indeed a revolutionary change, in the environment. The fulmar appears to have been expanding as fast as it can breed for two hundred years in our area. What obstacle has been removed?

The hypothesis which I present to you I do not claim particularly as my own, though I have given it some thought for some years. Bjárni Sæmundsson, the Iceland ornithologist, had much the same idea; and David Sergeant and R. M. Lockley and, I am sure, other marine ornithologists have been

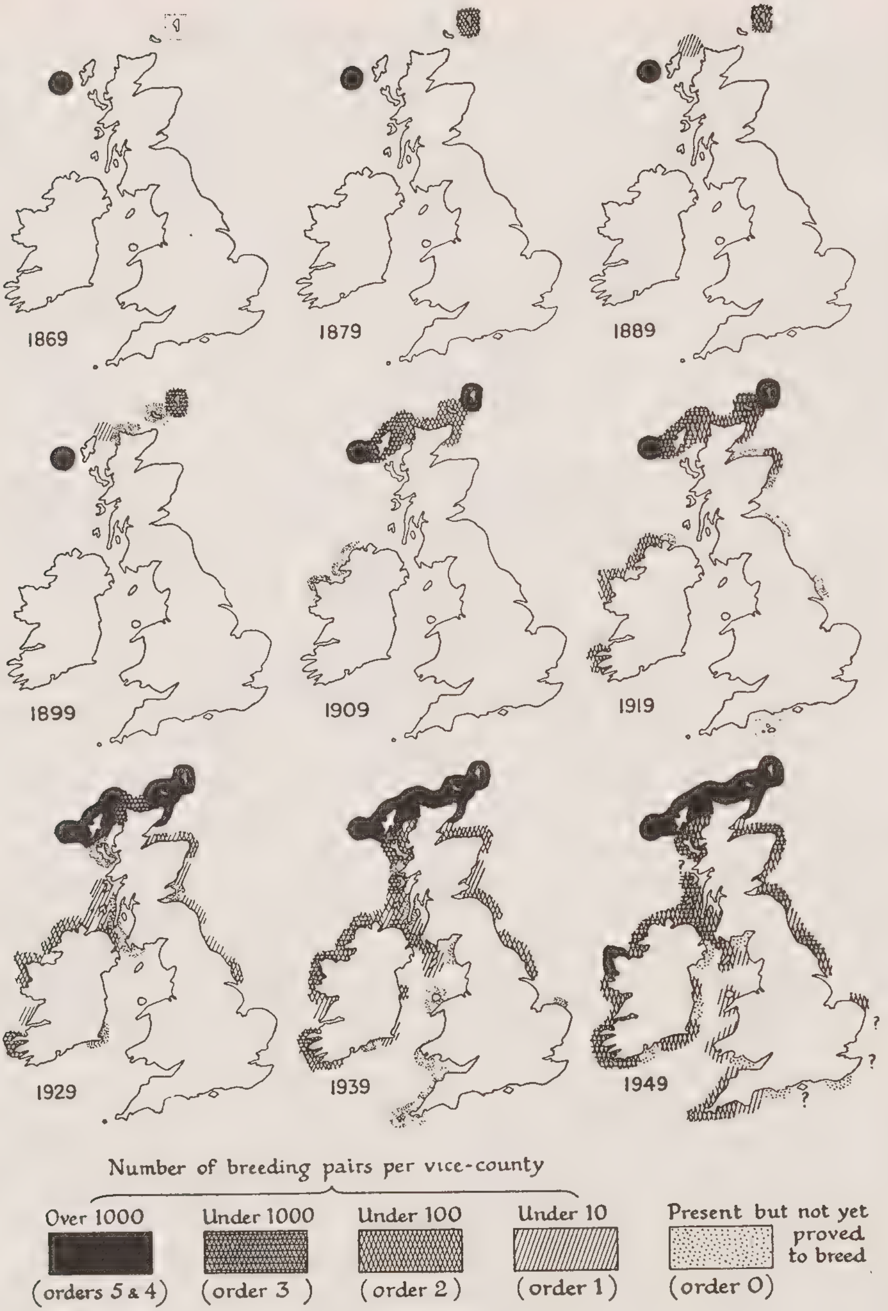


Fig. 5. The distribution of the breeding population of the fulmar in the British Isles, 1869–1949.

thinking on the same lines, and I have had valuable discussions with them. To come to the point: I do not believe there is a more economical hypothesis than that there has been a sudden and remarkable change in the food available to the fulmar; that man has been the provider of this food; and that the food has, to all intents and purposes, as far as the fulmar has been concerned, been unlimited. Such food has been the blubber, blood and offal of ship-side whaling, and is the guts, squids and coarse waste of the modern sea-going trawling that replaced it in time, if not in purpose.

The natural food of the fulmar appears to be what it can get; by which I mean that it is omnivorous, though it should be described primarily as a plankton-eater. It has been recorded as eating the remains and dung of bears, seals, many species of whales, several kinds of birds including fulmars, about five species of fish. Among the crustaceans it has eaten decapods, schizopods, cumaceans, isopods, amphipods, the cirripedes of whales and copepods. It eats annelids and chaetognaths including *Sagitta*, and the nematodes of its prey have been found in its stomach. It also takes cephalopods, alive and dead, and pteropods, particularly *Clione* and *Limacina*. It is among the few birds which eats ctenophores and scyphozoans, including the great jellyfish *Aurelia*, *Cyanea*, and probably also *Chrysaora*.

Its distribution at sea appears to march very closely with the distribution, as we know it, of these animals in the plankton. In particular very large concentrations of fulmars haunt the convergences of cold arctic and warm Atlantic water, which are rich in plankton, particularly the region at the tail of the Newfoundland Banks and that part of the Barents Sea north of the Varanger Fjord. Here fulmars feed all the year round, non-breeding birds, which I believe to be mainly young, remaining through the summer.

Let us now examine the whaling and trawling. The development of northern whaling, with ship-side flensing of right whales, dates from the discovery of Spitsbergen by William Barents in 1596. Whaling voyages started to it in 1610, and a thousand ships went to it in 1633. Friderich Martens, who sailed with the whaling fleet to Spitsbergen in 1671, describes, and draws a picture of, the crowd of fulmars that attended ship-side flensing. In the seventeenth century the inner Spitsbergen waters were fished out, and for about 200 years, from the middle of the seventeenth to the midle of the nineteenth centuries, the whalers hunted the sea and ice-edge, from Davis Straits, round Cape Farewell, through the Denmark Straits, past Iceland and Jan Mayen, up to about 79° off the east Greenland coast, across through Spitsbergen waters as far as Novaya Zemlya. But Davis Strait was not seriously hunted until about 1719, and the main arctic whaling appears to have been in what was called the West Ice (off the east Greenland coast) and particularly that part of it in the area Scoresby Sound-Jan Mayen-Iceland. This whaling was at its peak until about 1780 and began to decline markedly in 1821; though it went on rather desultorily, sometimes with a little success, until after the end of the nineteenth century.

The beginnings of the spread of the fulmar in Iceland, from Grímsey in the north to Westmann Islands in the south, seem to have coincided with much whaling in the 'west Ice' north of Iceland. The late nineteenth and twentieth century revivals of whaling (fin-whaling) at Spitsbergen, Norway, Iceland, Faeroe and Britain seems to have provided food for fulmars in some quantity, though probably not on the scale of the days of right-whaling, where flensing was done at ship's side. However, during the fin-whaling in Spitsbergen in the early years of the present century some flensing was done at ship's side, and some excellent photographs taken of many thousands of fulmars.

Trawling out of sight of land with ice—which means the gutting of fish at sea instead of in port, started in 1854; steam trawling in 1857. In 1875 the Great Fisher Bank was developed in the North Sea. In 1891 British fishermen discovered, and hastily exploited, the great trawling banks west of Iceland, and other grounds in the Norwegian Sea were found soon after. Since then trawling has expanded into a vast, new industry, that has already stubbed its toes once or twice on the 'law of over-fishing'. The great nineteenth century spurt of the fulmar population in Britain and east and north Iceland coincides with the revolution in trawling. It is not so easy to explain the spreads in south Iceland and Faeroe in the earlier part of the century; but we must note the development of coastal fishing then from these places.

For nearly a century, and particularly during the period of the greatest spread and increase of numbers of the fulmars, that is from about 1880 to the present day, *all* the fulmars of Iceland, Faeroe, Norway and Britain (and perhaps also those of Jan Mayen—which are also light-coloured) have had during the breeding season regular free meals of suitable food available within operational range of their colonies. I can risk suggesting that not a fortnight has passed (except in weather or war of exceptional severity) during the last fifty years, in which each of these fulmars has not had a trawler-crew gut a haul within reach of a food-flight. That the fulmars everywhere attend these guttings *in thousands* is something that every trawlerman knows, and that even ornithologists are now beginning to realise.

I must apologise for not having developed the march of the fulmars with whaling and trawling further; there is no time for detail, and I have been left to choose facts from a large collection. I hope to publish a full analysis in another place; but meanwhile offer for your criticism and discussion the suggestion that the fulmar is now a symbiote of man, still developing its relationship with him.

References: full references to the sources of the facts quoted in this account will be given in a forthcoming publication (The Fulmar: London, Collins, in press). Since the publication of the survey of the fulmar's spread up to 1939 (J. Fisher and G. Waterston, 1941, J. Anim. Ecol. 10: 204–72) much further informaton about its distribution has been collected by or through the British Trust for Ornithology, organized by the writer. Much information from Iceland has been collected by Dr Finnur Guðmundsson and others, to whom I am very grateful.

Histories of whaling and trawling have been written by J. Travis Jenkins, 1920, The Sea Fisheries, London, Constable; 1921, A History of the Whale Fisheries, London, Witherby.

*Discussion:*

J. S. Huxley: Could Mr Fisher tell us what would be the maximum percentage increase of a fulmar population in the absence of immigration? Could he also tell us what is the largest size of jellyfish attacked by fulmars?

J. Fisher: Supposing fulmars were immortal and perpetually fertile, and first bred when they were seven years old, the population of a closed community would increase at the rate of approximately 18 per cent. per annum. In practice, it would be reasonable to consider any observed increase in a population of more than 7 per cent. per annum to be due, at least partly, to immigration from without.

The largest size of jellyfish attacked by fulmars in the North Atlantic is *Cyanea capillata*. Fulmars also eat the large jellyfish *Aurelia aurita*. In the Pacific they have also been noticed eating a very large jellyfish, probably *Chrysaora*.

F. Salomonsen: In western Greenland a pronounced whaling took place from the 18th century until after 1850 but it does not appear that the number of colonies of the fulmar at that period was larger than now.

J. Fisher: Dr. Salomonsen, of course, knows more than anybody else about the fulmar colonies in Greenland. But, surely, we simply do not know whether there were more colonies of fulmars in West Greenland in the whaling days than there are now. The information from the old days is inadequate. However, a study of the ethnographical work of Franz Boas in Baffin Island shows that there are seven places on the island which bear the name *qaqodluin*, which is the Eskimo for "fulmar". Of these names, only three belong to places that are now certainly occupied by (two) fulmar colonies.[1] It is possible, therefore, that there were previously colonies in the Davis Strait and Baffin Bay region which are not now occupied by fulmars.

Dr. Salomonsen then pointed out that there was also at least one place named *qaqodluin* in the Disko area of West Greenland (on Arveprinsens Eiland) which is not now occupied by fulmars.

---

[1] The names are (1) qaqodluin = C. Charles York, at the north end of Baffin I.
(2) qaqodluin = C. Searle }
(3) qaqodloaping = Padloping } in eastern B. I.
(4) qaqodluin = an island in Exeter Sound, south-eastern B. I.
(5) qaqodlutang = Leopold Island, N. side entrance to Cumberland Gulf
(6) qaqodlualung = island near Quickstep Harbour, head of Cumberland G.
(7) qaqodluin = island near Cape Edwards, S. side entrace to Cumberland G.

Of these, (2) and (3) represent the known large colony C. Searle, and (6) a small fulmar colony discovered by L. Kumlien in 1878. No other is *known* to harbour a fulmar colony at present, though there is a large colony in Admiralty Inlet not very far from (1).

# The Present Population of the North Atlantic Gannet (Sula bassana)

*James Fisher and H. G. Vevers*

*Ashton* *Plymouth*
*England*

J. H. Gurney (1913) was the first worker to realise that it was practical to make an assessment of the number of nests occupied by all the world's North Atlantic gannets. His suggestion was that in about 1912 about 50 500 nests were occupied at the colonies then known to him. This was a slight under-estimate of the gannet population at that time, which was probably nearer 65 000 nests (Fisher and Vevers, 1943), but was a very careful effort to make the best of the information then available.

Using counts and estimates at the North Atlantic gannet colonies made between 1928 and 1935 (except for one not visited since 1914, and a small one unknown to them), Wynne-Edwards, Lockley and Salmon (1936) arrived at a figure of *c.* 78 000 occupied nests.

In 1939 an attempt to make a census, within the space of one breeding season, of the total number of nests occupied by North Atlantic gannets was organised by Fisher and Vevers (1943, 1944). In that year the gannets were breeding at twenty-two known colonies: twelve in Britain, one in Faeroe, three in Iceland, and six in the Gulf of St. Lawrence. One small colony in France in 1939 was unknown to us; with this exception all the colonies on the east side of the Atlantic, and two in the Gulf of St. Lawrence, had their nests counted in 1939. The four other St. Lawrence colonies were counted in 1934, 1936, 1940 and 1941, the 1941 colony not having been discovered previously. 83 022 nests were counted in all, of which 69 782 were on the east, and 13 240 on the west side of the Atlantic. (These figures differ by a negligible fraction from those published in 1943—44, owing to very small subsequent corrections.)

In 1949 we attempted to repeat the census of the nests on the east side of the Atlantic only, with the help of friends and correspondents. Most of the colonies of the gannet are difficult to reach, and for information we are particularly indebted to the many people who made journeys and counted on behalf of the census. Their names are given under the colonies which they visited. We must particularly thank H. G. Hasler, owner of the auxiliary yawl *Petula*, who took observers to the Bull Rock, the Little Skellig, Rockall, St. Kilda, Sula Sgeir and Sule Stack all in one season, a feat of amateur yachting which has not been surpassed. We give such information as we have about the number of nests occupied in years between 1939 and 1949; some of this relates to the foundation or extinction of a colony and is quite important.

The following is a list of the colonies of gannets in the eastern North Atlantic known to us between 1939 and 1949, with the numbers of nests counted (in some cases estimated).

1. ROUZIC; in les Sept Îles, off the coast of Brittany, France. Gannets first seen about between 1935 and 1938; colony established 1939, when twenty-five to thirty nests (unknown in 1939 census). Nests in 1945 about fifty, in 1946 and 1947 about 100, in 1948 about 150, in 1949 77 (D. Burckhardt, L. Hoffmann, R. M. Lockley, R. D. Etchécopar, J. Giban, l'Abbé Lebail and others).
2. ORTAC; near Alderney, Channel Isles. Founded in 1940, when one nest; about 250 in 1946, over 234 in 1948, 200 to 250 in 1949; 570 in 1950 (J. A. A. Wallace, R. Dobson, K. LeCocq, E. Quinain, J. Fisher, R. M. Lockley, B. M. Arnold).
3. LES ETACS; Alderney, Channel Isles. Date of foundation unknown — after 1940; but more gannets than usual had been seen about since 1936. About 200 nests 1946, 200 or more 1948, 418 in 1949; 615 in 1950 (as Ortac, also W. J. Lewis, L. Koch, E. M. Nicholson).
4. GRASSHOLM; Pembrokeshire, Wales. 5 875 nests in 1939; about 6 000 in 1946, 6 100–6 150 in 1947, 7 000 in 1948, at least 9 050 and possibly 9 500 in 1949 (E. J. M. Buxton, R. M. L., J. Barrett; R. A. F. photographs 1949).
5. GREAT SALTEE; Wexford, Eire. No definite nest 1939, though six birds about; one nest 1942; two pairs about, one nest 1943; one nest 1946 and 1947; two nests 1948 and 1949 (J. Barlee, J. Weaving, E. A. Constable, A. G. Mason, E. W. Ellis).
6. BULL ROCK; Cork, Eire. 575 nests 1939; 270 to 320 in 1949 (I. M. Goodbody from Hasler's *Petula*).
7. LITTLE SKELLIG; Kerry, Eire. 9 500 nests 1939; about 10 500 in 1946 (J. Barlee, overlapping round of photographs); about 12 000 in 1949 (I. M. G. from *Petula*, based on partial count).
8. BEMPTON CLIFFS; Yorkshire, England. Four nests in 1939; birds present but number of nests, if any, unknown 1941, 1942, 1943, 1944; no nest 1946, three in 1948, two or three in 1949 (Yorkshire Naturalists' Union, A. J. Wallis).
9. BASS ROCK; East Lothian, Scotland. 4 374 nests in 1939; 4 820 in 1949 (Midlothian Ornithological Club, G. Waterston).
10. GREAT SCAUR; Wigtownshire, Scotland. One nest in 1939; thirty-five to forty-five in 1945, *at least* twenty-eight in 1946, ninety in 1948, 100 in 1949 (C. E. Palmar, J. S. Crosthwaite, J. M. McWilliam).

11. AILSA CRAIG; Ayrshire, Scotland. 5 419 nests in 1939; 6 232 in 1940; 3 518 in 1941; 4 829 in 1942; 5 383 in 1947; 5 190 in 1948; 4 947 in 1949; 6 579 in 1950 (J. F., H. G. Vevers, J. A. Gibson, F. J. Huxley, V. A. Mitchison).
    [HOLY ISLE; by Arran, Scotland. Three birds seen 1946; birds carrying nesting-material 1947; about 17 roosting 1948; about 12 roosting and carrying nesting-material 1949; about 25 birds 1950, flying in and out of the cliffs, "possibly breeding" (J. A. G.).]
12. ST. KILDA; Outer Hebrides, Scotland. 16 900 nests in 1939; 17 035 in 1949 (J. F. from *Petula*).
    [ROCKALL; 191 miles west of St. Kilda. Up to fifteen near rock 1941. Twelve carrying nest-material and aimlessly dropping it; no nests 1949 (J. F. from *Petula*).]
13. SULA SGEIR; Outer Hebrides, Scotland. 3 970 nests in 1939; 6 182 in 1949 (I. D. Pennie, A. Huxley and F. J. H. from *Petula*).
14. SULE STACK; Orkney, Scotland. 3 490 nests in 1939; 2 010 in 1949 (as Sula Sgeir).
15. NOSS; Shetland, Scotland. 1 830 in 1939; about 3 230 in 1945; between 2 600 and 3 775 in 1946 (A. Clemetson, C. Lewis, R. Perry). No count 1949.
16. HERMANESS; Shetland, Scotland. 2 611 in 1939; nearing 4 000 in 1945 (A. C., C. L.); at least 3 750 in 1949 (L. S. V. Venables, based on partial count).
17. RUNDØ; near Aalesund, Statland, Norway. Founded about 1946, when four nests; seven in 1947; eight or nine in 1948 or 1949 (P. Valeur, H. Holgersen).
18. MYKINES HOLM, Faeroe. 1 473 in 1939; no later count.
19. WESTMANN ISLANDS (VESTMANNAEYJAR), S. Iceland. 4 359 in 1939, about the same in 1940, 5 538 in 1949 (J. F., H. G. V., J. S. Huxley, Þorsteinn Einarsson).
20. ELDEY, S. W. Iceland. 9 328 nests in 1939, about the same in 1941 and 1942; at least 11 000 in 1949 (as Westmann Islands; and Finnur Guðmundsson).
21. DRANGEY, N. Iceland. First known nest (one) in 1949 (F. G.).
    [GRÍMSEY, N. Iceland. Forty-five nests in 1939; deserted since 1946 (F. G.).]
22. RAUÐINUPUR, N. Iceland. Founded with one nest in 1944 or 1945; one nest in following year, six in 1949 (F. G.).
23. SKRÚÐUR, E. Iceland. Founded with one nest in 1943; one nest in 1944, about 150 in 1949 (F. G.).

Thus in 1939 the gannet on the east side of the North Atlantic occupied about seventy thousand nests at seventeen colonies, and in 1949 about eighty-two thousand nests at twenty-three colonies. This represents an increase of 18 per cent. in ten years, and a clear continuation of the steady upward trend in the gannet's population since it was at its lowest on the east side, at under fifty thousand nests, in 1889.

If this upward trend is reflected on the west side of the Atlantic (and the reported increases at Bonaventure Island in Quebec, the largest St. Lawrence colony, indicate that it is), then the North Atlantic gannet now occupies nearly a hundred thousand nests a year, and its May population of adults

| Colony | *Approximate* number of nests | | Remarks |
|---|---|---|---|
| | 1939 | 1949 | |
| Rouzic | 28[1] | 77 | Founded 1939 |
| Ortac | 0 | 225 | Founded 1940 |
| Les Etacs | 0 | 418 | Founded after Ortac |
| Grassholm | 5 875 | 9 200 | |
| Great Saltee | 0 | 2 | |
| Bull Rock | 575 | 295 | |
| Little Skellig | 9 500 | 12 000 | |
| Bempton Cliffs | 4 | 2 | |
| Bass Rock | 4 374 | 4 820 | |
| Great Scaur | 1 | 100 | Founded 1939 |
| Ailsa Craig | 5 419 | 4 947 | |
| St. Kilda | 16 900 | 17 035 | |
| Sula Sgeir | 3 970 | 6 182 | |
| Sule Stack | 3 490 | 2 010 | |
| Noss | 1 830 | 3 150 | (1946) |
| Hermaness | 2 611 | 3 750 | |
| Rundø | 0 | 8 | Founded *c.* 1946 |
| Mykines | 1 473 | 1 473 | (1939 total used) |
| Westmann Is. | 4 359 | 5 538 | |
| Eldey | 9 328 | 11 000 | |
| Drangey | 0 | 1 | Founded 1949 |
| Grímsey | 45 | 0 | Deserted since 1946 |
| Rauðinupur | 0 | 6 | Founded 1944 or 1945 |
| Skrúður | 0 | 150 | Founded 1943 |
| | 69 782 | 82 394 | |

is probably over two hundred thousand. This is a higher population than it has had since more than ninety years ago. The reasons for the increase remains, in our opinion, the same; the gannet is now only exploited regularly for human food in the Westmann Islands and on Mykines. In Britain no young gannets were taken in the war years on Sula Sgeir, but since the end of the war the men from Ness in Lewis have once more started their raids, in a tradition going back to the sixteenth century, and in 1949 they took a heavy crop from Sula Sgeir and some birds also from Sule Stack, which they had not raided since about 1932. Apart from these particular places where there are traditional harvestings the gannet is everywhere protected, and its protection appears to be paying dividends. The upper limit of population, which is presumably set by food-supply, does not appear to have been approached.

---

[1] Not included in census of 1939 as first published.

## References

Many notes on the gannets of particular colonies between 1939 and 1949 have been already published, under some of the names mentioned. The previous attempts at a world census of *Sula bassana* will be found in:

Fisher, J. and Vevers, H. G., 1943. The Breeding Distribution, History and Population of the North Atlantic Gannet (*Sula bassana*). Part I. A History of the Gannet's Colonies, and the Census in 1939. J. Anim. Ecol. 12: 173-213.

—— 1944. . . . Part II. The Changes in the World Numbers of the Gannet in a Century. J. Anim. Ecol. 13: 49-62.

Gurney, J. H., 1913. The Gannet. A Bird with a History. London, Witherby.

Wynne-Edwards, V. C., Lockley, R. M. and Salmon, H. M., 1936. The Distribution and Numbers of Breeding Gannets (*Sula bassana* L.). Brit. Birds, 29: 262-76.

# Increase and Decrease of the Breeding Range of Some Birds in Hungary

*A. Keve*
*Hungarian Ornithological Institute, Budapest*

*M. D. F. v. Udvardy*
*Zoological Institute, Uppsala*

From the five species noted, which had disappeared in Hungary before the beginning of the 18th century (cfr. Tab. 1), the Mediterranean species *Geronticus eremita* and *Anser aegypticus* bear witness to a much warmer climate here.

The disappearance of *Anas angustirostris, Nyroca rufina, Larus melanocephalus* and *Glareola nordmanni* in the 19th century cannot be occasioned by anthropogen changes in landscape, as the disappearance of *Pelecanus onocrotalus, P. crispus* and *Grus grus.*

In the present century the population of 8 Mediterranean, 4 Mongolian-mediterranean, 2 European and 1 Transpalearctic species diminished to the limit of total extermination. The connection between the diminishing of the heron species and the progress of civilization is evident. Preservation measures saved the last remains of their stock. In the case of other waterfowl (e.g. *Plegadis falcinellus*) the final cause was in general the quantitative diminishing of the biotopes on which they were living. However, civilization could have no fatal influence on the habitats of *Tringa stagnatilis, Glareola pratincola, Chlidonias hybrida, Gelochelidon nilotica, Himantopus himantopus* and *Recurvirostra avosetta*; on the contrary the salt steppes and lakes were considerably enlarged due to river regulation.

There are no breeding reports of *Otis tetrax* since 1918, though *Otis tarda* thrives well on the "Kultursteppe." Recently *Emberiza hortulana* kept away from its breeding places around Budapest after the severe winter 1928/29, while *Ciconia ciconia* diminished after the drought of 1945–47.

*Carduelis spinus, Turdus pilaris* and *Numenius arquatus* are advancing from the northwest to the Hungarian Plain. It cannot be a mere coincidence that their breeding data stay in good correlation, as can be seen from a few reports between 1892–1907, and regularly from 1928, 32, 33 respectively. *Circus pygargus* has come from the same direction, but has recently been

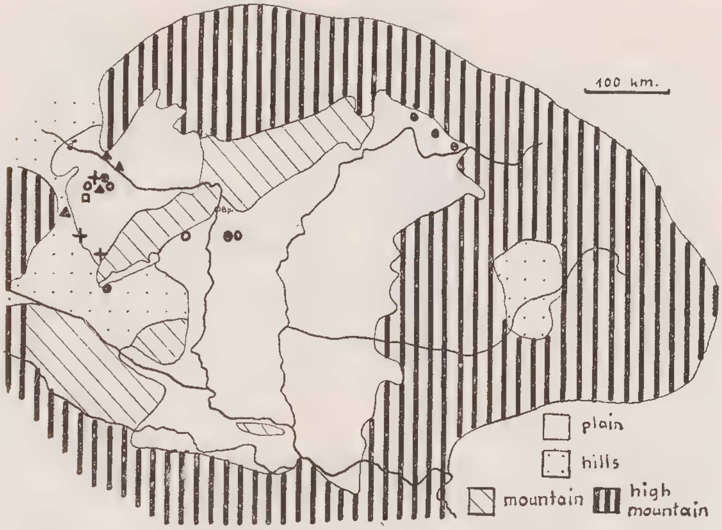


Fig. 1. Breeding distribution of some birds, which have advanced to the Hungarian Plain from NW. *Carduelis spinus:* ▲, *Anthus pratensis:* □, *Turdus pilaris:* +, *Circus pygargus:* ●, *Numenius arquatus:* ○.

reported from the feet of the NE Carpathians too. Furthermore *Anthus pratensis* must be mentioned, doubtful data 1852 and 1883, reliable observations between 1932–42. (Fig. 1).

*Serinus serinus* flooded Transylvania about 1880–1920, and later the Plain as well, together with *Phoenicurus phoenicurus.*

Three new breeding birds entered from the south exactly in the same manner, but with enormous velocity. *Dryobates syriacus* was discovered at the lower Danube in 1928. In 1937 it appeared 130 km farther north, in the present year it reached the hills north of Budapest. The expansion was fan-like, with S-N axis. In 22 years 260 km of northward expansion were noted, the speed being about 11 km/year.

It only took *Hippolais pallida* 13 years to reach Budapest from the same expansion centrum, which gives a speed of 19 km/year. Much more striking and quicker was the range-increase of *Streptopelia decaocto.* Its breeding in Belgrade was well known since 1912, but it never crossed the Danube. In 1932 it suddenly appeared in three places in Central Hungary. In 15 years it advanced fan-like and has settled in Hungary in such quantities, that to-day there is hardly a village without breeding birds (Fig. 2).

To make the influence of the decreasing and increasing species clear, we shall survey the distribution of the breeding birds of the Carpathian

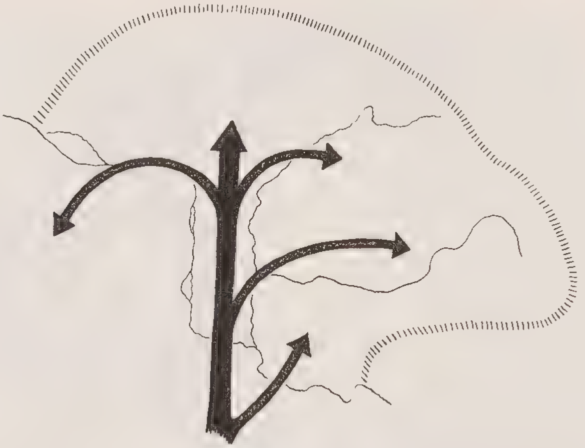


Fig. 2. The expansion of *Streptopelia d. decaocto* in Hungary.

Basin with regard to their zoogeographical classification according to Stegmann, Kalela etc. Extrapalearctical distributions will not be considered.

The majority of the ornis consist of the European species, in the Carpathian mountains as well as in the Basin. The relative number of the Transpalearctical elements are also the same (birds distributed in the whole Palearctis, or at least in a broad belt from the Atlantic to the Pacific coast). The Siberian species give 6 % of the Carpathian fauna, but only 2.5 % of that of the Basin. Recently an Arctic species, *Anser albifrons* has been summering here in small numbers, and in 1948 breeding was ascertained too. Birds of the Mediterranean and Mongolian-Mediterranean groups form 1/6 of the Carpathian fauna, but nearly 1/4 of the Basin. 40 % of the species in the last two groups reach the W or NW boundary of their breeding range in Hungary. Consequently they connect the Carpathian Basin with the East European-South Asian steppe. Nevertheless, there are many more species there which do not extend as far as Hungary. Only 14 species, i. e. 42 % of the Mediterranean-Mong.-Mediterranean birds of the Pontic steppes (Stegman) are now living in Hungary. Phytopaleontological and phytogeographical research prove that the present large steppes of the Hungarian Plain are of secondary character, the original climatic climax formation since the beginning of the subboreal age having been oak forest and wooded steppe. Grassy steppe only existed in some spots where the local conditions did not allow the growth of forests. This is supported by our statement above concerning the absence of many steppe birds. The absence of the stenotopic larks (*Melanocorypha calandra, M. yeltonensis, M. sibirica, Calandrella ru-*

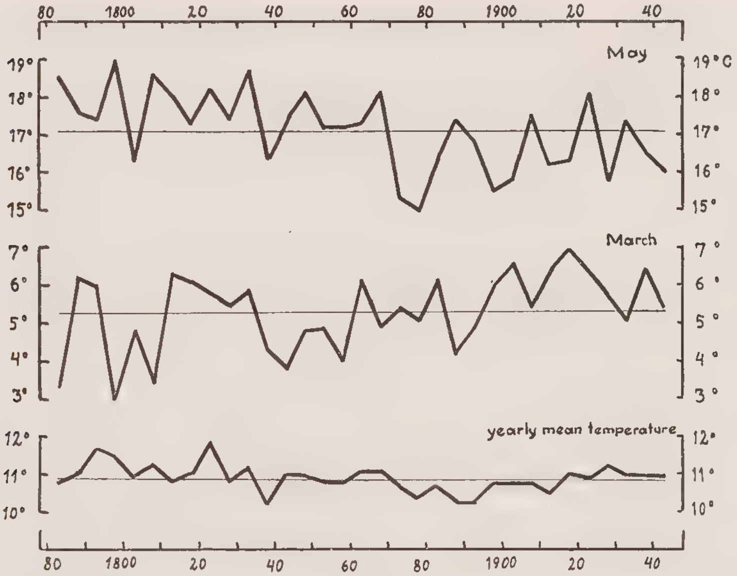


Fig. 3. Yearly and monthly mean temperature curves for Budapest 1780–1945.

*fescens*) seems particularly noteworthy, only *Calandrella cinerea* having perhaps bred here in the last century, and having been observed during the last two decades. On the other hand the number of steppe-species might permit one to assume that numerous large steppe "spots" made their survival possible.

The most inconstant groups are the Mediterranean and Mongolian-Mediterranean. Of these species 16.3 % is increasing, 30.6 % decreasing in number. However, these changes do not show any such clear relationship to the recent climatic changes, as those of the corresponding species of N. and W. Europe.

The annual average temperature of Budapest seems to have fallen since the 1830's, reaching a minimum about 1880–90, and a recent rise since the 1920's (Fig. 3). The summer months have grown considerably cooler from the 1880's to the 1930's, the minima combined with precipitation tops. In the same period, winter and early spring became distinctly warmer, without greater changes in precipitation. In this period of maritimization of the summer climate, the great diminishing of the species mentioned above occurs, among them 13 Mediterranean and Mongolian-Mediterranean, and at least as far as the six species which could not be greatly influenced by civilization are concerned, the sole possible reason seems to be the climatic change. The last increase in temperature explains the wintering of *Cettia*, and the increase of the *Merops apiaster* population. Evidently the warm winters promoted the spreading of the resident *Dryobates syriacus* and *Streptopelia decaocto* (this later species breeds in Hungary in favorable years already in March and until November). The expansion of *Hippolais pallida* does not seem to be in any correlation with the climatic data.

The expansion of the four European species, which simultaneously immigrated from NW, coincides with the beginning of cooler, more humid summers. All these species live NW and N of Hungary, in cooler, more humid parts of Europe. The Northwest is that part of Hungary which is most affected by the oceanic climate, only there does one find heaths and marshy meadows of the western European type. Thus even before the change, this landscape was closer to that of the biotopes where these birds live, and some of them found their way to it when the climate became more favourable.

An excellent example of the direct climatic influence is the enormous increase of the *Egretta alba* population in 1949: at the same time the late Pateff informed us (in litt.) that in Bulgaria a terrific drought occurred, drying out all the breeding places of herons.

Changes in population dynamics have been most influential in the immigration of southeastern elements. An excellent example is *Streptopelia decaocto*, which did not cross the Danube for 20 years but in the next 18 years spread many hundred kilometers. Its new settlements are far from the original starting point.

But population depression can be of influence as well as population dynamics. When a population becomes unable to adapt itself to the waves of ecological effects fluctuating on the borders of the area of occurrence, one unfavorable factor, viz. human activity, climatic influence, or anything else will suffice to make the species disappear from the area in question. This might explain the disappearance of the Northern species *Lyrurus tetrix*, and of many Southern species.

## Table I. Birds Which Have Disappeared and Diminished in the Carpathian Basin.

I. Disappeared before 1800:

| | | |
|---|---|---|
| MED. | *Geronticus eremita.* | Disappeared in the 17th century. |
| SIB. | *Cygnus cygnus.* | Still breeding in the 18th century. |
| EU. | *Cygnus olor.* | Still breeding in the 18th century. |
| MED. | *Chenalopex aegypticus.* | At the beginning of the 18th century. |
| MO-MED. | *Tadorna tadorna.* | At the beginning of the 18th century. |

II. Disappeared between 1800–1850:

| | | |
|---|---|---|
| MED. | *Nyroca rufina.* | Last breeding date 1847. |
| MO-MED. | *Glareola nordmanni.* | In 1841 and 1843 bred in Hungary. |

III. Disappeared between 1850–1900:

| | | |
|---|---|---|
| MO-MED. | *Pelecanus onocrotalus.* | Last breeding date 1873. |
| MO-MED. | *Pelecanus crispus.* | Last breeeding date 1868. |
| MED. | *Anas angustirostris.* | Observed 1893-96. |
| EU. | *Grus grus.* | Last breeding 1892. |
| MED. | *Larus melanocephalus.* | 1847, maybe 1878 bred, 1903 observed. |
| SIB. | *Lyrurus tetrix.* | Disappeared successively between 1870–1896. |

IV. Species diminishing since the 1880's:

EU.: *Platalea leucorodia, Egretta alba.*

MED.: *Plegadis falcinellus, Egretta garzetta, Ardeola ralloides, Phalacrocorax pygmeus, Glareola pratincola, Otis tetrax, Chlidonias hybrida, Gelochelidon nilotica.*

MO-MED.: *Aquila heliaca, Tringa stagnatilis, Himantopus himantopus, Recurvirostra avosetta.*

TRANSP.: *Phalacrocorax carbo.*

Further several larger waterfowls and birds of prey diminishing in consequence of civilization and urbanization.

## Table II. New Species in the Carpathian Basin since the 1880's.

ARCT.: *Anser albifrons* (1940) 1948.

SIB.: *Turdus pilaris* 1901.

EU.: *Carduelis spinus* 1895, *Anthus pratensis* 1932 (already 1852, 1883?), *Circus pygargus* 1886, *Numenius arquatus* 1907 (The 1880's?).

MED.: *Hippolais pallida* 1937, *Dryobates syriacus* 1928, *Streptopelia decaocto* 1932.

Increasing species.

MED.: *Serinus c. serinus*, the 1920's, *Merops apiaster* 1948.

MO-MED.: *Calandrella cinerea*, the 1930's, *Phoenicurus ochruros*, the 1920's.

TRANSP.: *Asio accipitrinus*, the 1930's.

## Table III. Zoogeographical Classification of the Breeding Bird Species of the Carpathian Mountains.

Arctic species: *Charadrius morinellus* (1).

Siberian species: *Nucifraga caryocatactes, Pyrrhula pyrrhula, Loxia curvirostra, Parus atricapillus, Muscicapa parva, Turdus pilaris, Picoides tridactylus, Dryocopus martius, Aegolius funereus, Glaucidium passerinum, Strix uralensis, Lyrurus tetrix, Tetrao urogallus, Tetrastes bonasia* (14).

European species: *Corvus corone, C. frugilegus, Coloeus monedula, Pica pica, Garrulus glandarius, Sturnus vulgaris, Oriolus oriolus, Coccothraustes coccothr., Chloris chloris, Carduelis*

*carduelis, C. spinus, C. cannabina, Fringilla coelebs, Emberiza calandra, E. citrinella, E. hortulana, Lullula arborea, Anthus trivialis, Motacilla cinerea, M. alba, Certhia familiaris, C. brachydactyla, Parus major, P. caeruleus, P. ater, P. cristatus, P. palustris, Regulus regulus, Lanius minor, L. collurio, Muscicapa striata, M. hypoleuca, M. albicollis, Phylloscopus trochilus, Ph. sibilatrix, Locustella fluviatilis, L. naevia, Acrocephalus arundinaceus, A. scirpaceus, Hippolais icterina, Sylvia nisoria, S. borin, S. atricapilla, S. communis, S. curruca, Turdus viscivorus, T. ericetorum, T. torquatus, T. merula, Saxicola rubetra, Phoenicurus phoenicurus, Luscinia megarhyncha, L. luscinia, Erithacus rubecula, Prunella modularis, Troglodytes troglodytes, Cinclus cinclus, Apus apus, Caprimulgus europaeus, Upupa epops, Coracias garrulus, Alcedo atthis, Picus viridis, P. canus, Dryobates medius, Otus scops, Strix aluco, Tyto alba, Aquila clanga, A. pomarina, Hieraëtus pennatus, Circus cyaneus, Milvus milvus, M. migrans, Pernis apivorus, Circaëtus gallicus, Ciconia ciconia, C. nigra, Ixobrychus minutus, Columba oenas, C. palumbus, Streptopelia turtur, Scolopax rusticola, Crex crex, Gallinula chloropus, Perdix perdix, Coturnix coturnix* (87).

Mediterranean species: *Serinus c. serinus, Emberiza cirlus, E. cia, Parus lugubris, Oenanthe hispanica, Merops apiaster, Neophron percnopterus, Gyps fulvus, Streptopelia decaocto* (9).

Mongolian-Mediterranean species: *Galerida cristata, Alauda arvensis, Anthus campestris, Monticola saxatilis, Saxicola torquata, Phoenicurus ochruros, Athene noctua, Falco naumanni, F. vespertinus, Aquila heliaca, Circus aeruginosus, Aegypius monachus, Vanellus vanellus, Charadrius dubius, Alectoris graeca* (15).

Transpalearctic species: *Corvus corax, Passer domesticus, P. montanus, Emberiza schoeniclus, Motacilla flava, Sitta europaea, Aegithalos caudatus, Lanius excubitor, Phylloscopus collybita, Oenanthe oenanthe, Hirundo rustica, Delichon urbica, Riparia riparia, Dryobates major, D. leucotos, D. minor, Jynx torquilla, Cuculus canorus, Bubo bubo, Asio otus, Falco peregrinus, F. subbuteo, F. tinnunculus, Aquila chrysaëtus, Buteo buteo, Accipiter gentilis, A. nisus, Haliaëtus albicilla, Pandion haliaëtus, Anas platyrhynchos, A. crecca, Tringa hypoleucos* (32).

Tibetan species: *Pyrrhocorax graculus, Anthus spinoletta, Tichodroma muraria, Prunella collaris, Gypaëtus barbatus* (5).

## Table IV. Zoogeographical Classification of the Breeding Bird Species in the Carpathian Basin.

Arctic species: *Anser albifrons* (1).

Siberian species: *Muscicapa parva, Turdus pilaris, Dryocopus martius, Anas acuta, Philomachus pugnax, Tetrastes bonasia* (6).

European species: *Corvus corone, C. frugilegus, Coloeus monedula, Pica pica, Garrulus glandarius, Sturnus vulgaris, Oriolus oriolus, Coccothraustes cocc., Chloris chloris, Carduelis carduelis, C. spinus, C. cannabina, Fringilla coelebs, Emberiza calandra, E. citrinella, E. hortulana, Lullula arborea, Anthus trivialis, A. pratensis, Motacilla cinerea, M. alba, Certhia familiaris, C. brachydactyla, Regulus regulus, Parus major, P. caeruleus, P. palustris, Lanius minor, L. senator, L. collurio, Muscicapa striata, M. hypoleuca, M. albicollis, Phylloscopus trochilus, Ph. sibilatrix, Locustella fluviatilis, L. luscinioides, L. naevia, Acrocephalus arundinaceus, A. scirpaceus, A. palustris, A. schoenobaenus, Hippolais icterina, Sylvia nisoria, S. borin, S. atricapilla, S. communis, S. curruca, Turdus viscivorus, T. ericetorum, T. merula, Saxicola rubetra, Phoenicurus phoenicurus, Luscinia megarhyncha, L. luscinia, Erithacus rubecula, Prunella modularis, Troglodytes troglodytes, Cinclus cinclus, Apus apus, Caprimulgus europaeus, Upupa epops, Coracias garrulus, Alcedo atthis, Picus viridis, P. canus, Dryobates medius, Otus scops, Strix aluco, Tyto alba,* *Aquila clanga, A. pomarina, Hieraëtus pennatus, Circus cyaneus, C. pygargus, Milvus milvus, M. migrans, Pernis apivorus, Circaëtus gallicus, Ciconia ciconia, C. nigra, Platalea leucorodia, Egretta alba, Ixobrychus minutus, Nyroca ferina, N. nyroca, Podiceps griseigena, P. nigricollis, P. ruficollis, Columba oenas, C. palumbus, Streptopelia turtur, Numenius arquatus, Scolopax rusticola, Capella gallinago, Chlidonias nigra, C. leucoptera, Sterna hirundo, S. albifrons, Rallus aquaticus, Porzana porzana, P. pusilla, P. parva, Crex crex, Gallinula chloropus, Perdix perdix, Coturnix coturnix* (107).

Mediterranean species: *Pastor roseus, Serinus c. serinus, Lusciniola melanopogon, Hippolais pallida, Luscinia svecica cyan., Merops apiaster, Dryobates syriacus, Gyps fulvus, Plegadis falcinellus, Ardea purpurea, Egretta garzetta, Ardeola ralloides, Nycticorax nycticorax, Oxyura leucocephala, Phalacrocorax pygmeus, Streptopelia decaocto, Burhinus oedicnemus, Glareola pratincola, Otis tetrax, Chlidonias hybrida, Gelochelidon nilotica* (21).

Mongolian-Mediterranean species: *Calandrella cinerea, Galerida cristata, Alauda arvensis, Anthus campestris, Remiz pendulinus, Panurus biarmicus, Monticola saxatilis, Saxicola torquata, Phoenicurus ochruros, Athene noctua, Falco cherrug, F. vespertinus, F. naumanni, Aquila heliaca, Circus aeruginosus, C. macrourus, Aegypius monachus, Botaurus stellaris, Anser anser, Charadrius dubius, C. alexandrinus, Vanellus vanellus, Tringa totanus, T. stagnatilis, Himantopus himantopus, Recurvirostra avosetta, Limosa limosa, Otis tarda* (28).

Transpalearctic species: *Corvus corax, Passer domesticus, P. montanus, Emberiza schoeniclus, Motacilla flava, Sitta europaea, Aegithalos caudatus, Lanius excubitor, Phylloscopus collybita, Oenanthe oenanthe, Hirundo rustica, Delichon urbica, Riparia riparia, Dryobates major, D. leucotos, D. minor, Jynx torquilla, Cuculus canorus, Bubo bubo, Asio otus, A. accipitrinus?, Falco subbuteo, F. tinnunculus, Aquila chrysaëtus, Buteo buteo, Accipiter gentilis, A. nisus, Haliaëtus albicilla, Pandion haliaëtus, Ardea cinerea, Anas platyrhynchos, A. crecca, A. querquedula, A. strepera, Spatula clypeata, Phalacrocorax carbo,. Podiceps cristatus, Tringa hypoleucos, Larus ridibundus, Fulica atra* (40).

## Table V. Classification of the Breeding Bird Fauna in Zoogeographical Groups.

In the Carpathian Mountains:

| | | |
|---|---|---|
| *Arctic species* | 1 | 0.61 % |
| *Siberian species* | 14 | 8.59 |
| *European species* | 87 | 53.38 |
| *Mediterranean species* | 9 | 5.52 |
| *Mongolian-Mediterranean species* | 15 | 9.20 |
| *Tibetan species* | 5 | 3.07 |
| *Transpalearctic species* | 32 | 19.63 |
| | 163 species | 100.00 % |

In the Carpathian Basin:

| | | |
|---|---|---|
| *Arctic species* | 1 | 0.50 % |
| *Siberian species* | 6 | 2.97 |
| *European species* | 107 | 52.47 |
| *Mediterranean species* | 21 | 10.40 |
| *Mongolian-Mediterranean species* | 28 | 13.86 |
| *Transpalearctic species* | 40 | 19.80 |
| | 203 species | 100.00 % |

## References

Feriang, O., 1948. Sylvia IX–X. 33.

Kalela, O., 1946. Ann. Ac. Sci. Fenn. Ser. A. IV. 12, pp. 81.

—— 1946. Ornis Fennica 23, 77.

—— 1949. Bird Banding 20, 77.

Keve, A., 1948. Ibis 90, 465.

—— 1948. Sylvia IX–X. 97.

Larsen, A., 1949. Dansk. Orn. For. Tidsskr. 43, 129.

Reinikainen, A., 1947. Arch. Soc. Zool. Bot. Fenn. Vanamo, 2, 131.

Réthly, A., 1947. The Climate of Budapest, pp. 147. Budapest.

Salomonsen, F., 1948. Dansk Orn. For. Tidsskr. 42, 85.

Schenk, J., 1918. Aves, in: Fauna Regni Hungariae, pp. 112, Budapest.

Stegman, B., 1938. Principes généraux des subdivisions ornithogéographiques de la région paléarctique. Fauna U.R.S.S. Oiseaux I, pp. 157. Leningrad.

Udvardy, M., 1942. Tisia V, 92.

Further the Hungarian avifaunistic literature, especially in Aquila I–LIV, 1893–1950.

# Beobachtungen über Klimaveränderungen und Bestandsveränderungen einiger Vogelarten in Nordwestdeutschland

*J. Peitzmeier*

*Warburg i. Westfalen*

Die Tatsache, dass auf dem X. Internationalen Ornithologischen Kongress eine ganze Anzahl von Vorträgen gehalten werden, die die Beziehungen zwischen Klimaveränderungen und Bestandsbewegungen innerhalb der Vogelwelt zum Gegenstand haben, beweist für sich schon die Aktualität dieser Frage.

Früher schon hat Kalela sich in einer Reihe von Arbeiten mit diesem Fragenkomplex vor allem bezüglich der Verhältnisse in Finnland beschäftigt und in einer seiner letzten einschlägigen Veröffentlichungen (1946) die Wichtigkeit der Sammlung des Materials betont, das zur Beleuchtung dieser Frage für mitteleuropäische Populationen dienen kann.

Ich möchte daher in aller Kürze über Beobachtungen berichten, die über Klimaveränderungen und Bestandsveränderungen in Nordwestdeutschland gemacht werden konnten, wobei zu berücksichtigen ist, dass solche Einflüsse sich in Mitteleuropa weniger bemerkbar machen als im Norden. Ich beschränke mich dabei im wesentlichen auf das Gebiet der Münsterschen Tieflandsbucht in Westfalen mit einer Ausweitung nach Westen, ein Gebiet, das im Nordosten durch den Teutoburgerwald, im Süden durch den Haarstrang und im übrigen etwa durch die Städte Paderborn, Recklinghausen, München—Gladbach, Kleve und Rheine begrenzt wird.

Dieses Gebiet erweist sich aus zwei Gründen als besonders geeignet für solche Untersuchungen: Einmal ist es ein Übergangsgebiet zwischen ozeanischem und kontinentalem Klima, und in einem Übergangsgebiet müssen Änderungen dieser Art jeweils zunächst und besonders deutlich zutage treten, zum anderen sind wir durch die Arbeiten von Landois (1886) und Koch (1924) über den früheren Bestand bezw. die Veränderungen des Bestandes seit den 80er Jahren des vergangenen Jahrhunderts besonders gut unterrichtet.

Ich selbst beobachte in diesem Gebiet seit 1914 und wurde und werde dabei durch eine Anzahl münsterländischer Ornithologen und in letzter Zeit darüber hinaus von Mitgliedern der Nordrhein-westfälischen Ornithologischen Arbeitsgemeinschaft unterstützt, die hier einzeln nicht genannt werden können.

Das Ergebnis dieser Beobachtungen ist folgendes: Es konnten charakteristische Bestandsbewegungen beobachtet werden und zwar an den wärmebedürftigen Arten: das sind einmal die „kontinentalen" Arten und dann die spät heimkehrenden Zugvögel.

Diese Bestandsbewegungen verliefen so, dass seit etwa 1900, vor allem aber nach 1915, eine im grossen ziemlich stetige Abnahme erfolgte, die bei einigen Arten sogar fast bis zum Verschwinden führte, dass diese Arten sich dann seit etwa 1934 erholten und bis zur Gegenwart vermehrten, besonders deutlich seit 1945.

Wie gesagt, möchte ich die betroffenen Arten in zwei Gruppen einteilen, einmal die spät eintreffenden Zugvögel, die durch ihr spätes Ankommen ein erhöhtes Wärmebedürfnis verraten, dann die Arten, die zwar Standvögel oder früh eintreffende Zugvögel sind, aber im kontinentalen Klima ihr Verbreitungszentrum haben.

Über die Angehörigen der ersten Gruppe ist im einzelnen zu sagen[1]: *Jynx torquilla* war nach Koch (1924) vor „langen Jahren" sehr häufig im Münsterlande. Landois (1886) spricht aber schon 1886 von einer Abnahme, die er auf menschliche Einflüsse zurückführt. Nach Koch verschwindet der Vogel allmählich. Ich selbst habe bis 1930 kein Brutpaar angetroffen. Die Art war im Gebiet fast ausgestorben. Seit 1940 ist an vielen Orten eine deutliche Zunahme bemerkbar (vgl. auch Kuhlmann 1950), besonders auffallend im Westen, im Gebiet des Niederrheins. Dort ist er vor allem seit 1943 häufiger aufgetreten, besonders zahlreich 1946 und 1947.

*Lanius collurio.* Zur Zeit Landois' war der Neuntöter noch überall häufiger Brutvogel. Er ist dann immer mehr zurückgegangen (Koch). Ich fand in meinem Beobachtungsgebiet bis 1930 nur höchst selten ein Brutpaar. Seit 1940 hat die Art zugenommen, besonders seit 1945.

*Streptopelia turtur* war zu Landois' Zeiten überall häufig, nach Koch sehr häufig, hat sich nach ihm „in den letzten Jahren" sehr vermindert (das schrieb er 1923). Dieser Rückgang hielt nach meinen Beobachtungen bis gegen Ende der 20er Jahre an. In den 30er Jahren hat sich die Art sehr stark vermehrt. Das gilt auch für den Westen.

*Delichon urbica.* Diese früher im Münsterlande sehr häufige Schwalbe ging nach Koch und meinen Beobachtungen im 2. und 3. Jahrzehnt ganz rapid zurück und war um 1930 aus meinem Beobachtungsgebiet nahezu verschwunden. Seit etwa 1935 nimmt die Art langsam aber stetig wieder zu.

---

[1] Bei der deutlich zutage tretenden Vermehrung erübrigten sich Bestandszählungen, die ausserdem auch für die erste Periode nicht vorlagen.

Das gleiche gilt für *Muscicapa striata.*

*Emberiza hortulana* kam in den 80er Jahren im Münsterlande lokal häufig vor. Aus meinem Beobachtungsgebiet, wo der Vogel vorher nicht selten war, verschwand er nach 1915 völlig. Seit Mitte der 30er Jahre nahm er örtlich wieder zu, und seit etwa 1939 erfolgte in dem Gebiet, wenigstens lokal, eine weitere Zunahme.

*Upupa epops.* Bei kaum einer Art war der Bewegungsrhythmus so auffallend wie beim Wiedehopf. Er kam gegen Ende des vorigen Jahrhunderts nach Landois in der ganzen Provinz vor, wenn auch meist spärlich. Sehr häufig war er dagegen in der Senne und ihrem Umkreis, Gebiete, die meinem Beobachtungsgebiet benachbart sind. Auch in diesem war der Wiedehopf bis etwa 1915 häufig. Dann verschwand er dort völlig, hielt sich zunächst noch in der Senne. Aber auch hier wurde von 1931 bis 1941 kein Brutpaar mehr gefunden (Kuhlmann 1950). Seit 1941 nimmt die Art wieder ständig zu. 1946 brüteten allein auf dem Truppenübungsplatz 10–12 Paare (Goethe 1948). Auch in weiteren Gegenden des Münsterlandes wurden in den letzten Jahren wieder Wiedehopfe beobachtet.

*Coracias garrulus.* Es ist in diesem Zusammenhang erwähnenswert, dass die Blauracke, die zwar im Münsterlande schon um die Mitte des vorigen Jahrhunderts ausstarb, neuerdings sich in benachbarten Teilen Nordwestdeutschlands, wo sie vor 1900 verschwand, anscheinend wieder auszubreiten beginnt. Jedenfalls wurden 1948 im Landkreis Celle und 1948 und 1949 im Kreise Gifhorn wieder Brutpaare gefunden (Tietge 1949, Willke 1949).

Zur zweiten Gruppe gehören nur wenige Arten.

Auffallend ist die seit 1944 in Südost—Westfalen sehr zügig fortschreitende Ausbreitung des *Turdus pilaris.* Wenn diese kontinentale Art auch seit 100 Jahren immer weiter nach Westen vordringt, so kann diese jetzt in Westfalen zu beobachtende starke Expansion doch auch für unsere Frage Interesse beanspruchen. Die Drossel rückt hier nach meinen seit 1944 im Gange befindlichen Untersuchungen mit einer Durchschnittsgeschwindigkeit von 5 km pro Jahr in Flusstälern vor und vermehrt sich stark.

*Columba oenas.* Die Art, die früher in der Münsterischen Ebene im allgemeinen nur spärlich vorkam, hat in den 40er Jahren sehr deutlich zugenommen und ist, da passende Höhlen oft fehlen, gelegentlich zum Freibrüten übergegangen. Auch am Niederrhein hat sie sich in den beiden letzten Jahrzehnten, bzw. erst seit 1946 vermehrt.

*Emberiza calandra* ist in die Sandgebiete des Münsterlandes um 1870 eingewandert und hat sich dort zunächst vermehrt. Ab 1900 ging die Art ständig zurück (Koch). In meinem Beobachtungsgebiet, wo sie noch um 1915 nicht selten war, verschwand sie um 1930, tauchte um 1940 wieder auf und vermehrt sich — durch die strengen Winter zurückgeworfen — langsam.

Ähnlich verhält es sich mit *Galerida cristata*. Ihr Bestand ging nach Koch und meinen Beobachtungen etwa im 2. u. 3. Jahrzehnt unseres Jahrhunderts sehr stark zurück. In meinem Beobachtungsgebiet sah ich Jahrzehnte hindurch kein Exemplar. Etwa seit 1946 ist eine — allerdings sehr langsame — Zunahme zu verzeichnen. Es wurden mir mehrere besetzte Brutplätze bekannt, die Jahrzehnte hindurch verwaist waren.

Zur Abrundung sei noch hingewiesen auf das, wenn auch bisher vereinzelt gebliebene Vorkommen von *Phylloscopus bonelli* im Harz, im Teutoburger Wald und im Süntel 1947, also erheblich nördlicher als bisher nachgewiesen (Bruns 1948), auf die wiederholte Beobachtung (1948, [?]1949, 1950) von *Himantopus himantopus* in Westfalen (Söding 1950) und auf das sensationelle Vordringen der *Streptopelia decaocto* als Brutvogel bis nach Westfalen und Niedersachsen. *Oriolus oriolus* hat stellenweise im letzten Jahrzehnt sich vermehrt. Anscheinend nimmt *Pernis apivorus* zu (Goethe 1948).

Bestandsschwankungen sind bei Vögeln etwas durchaus Gewöhnliches. Wenn diese Bestandsschwankungen aber in gleichsinniger Weise über einen grösseren Zeitraum hin eine ganze Reihe von Arten betreffen, so muss diesen Bewegungen eine gemeinsame besondere Ursache zu Grunde liegen. Und wenn es sich bei allen von diesem Auf und Ab betroffenen Arten um wärmebedürftige Vögel handelt, dann liegt die Vermutung nahe, dass für diese Bestandsbewegungen klimatische Faktoren verantwortlich sind.

Wie war in dem behandelten Zeitraum das Klima in Nordwestdeutschland?

Nach einer zusammenfassenden Arbeit über Klimaschwankungen in Nordwestdeutschland von Ringleb (1940) wurde in dem Zeitraum von etwa 1900–1930 das Klima ozeanischer. Für unsere Frage ist besonders bedeutungsvoll, dass zwar die Monate März und Mai eine Temperatursteigerung, April und Juni dagegen eine Abnahme erfuhren. Dabei ist zu beachten, dass die Apriltemperatur erst seit 1915 herunterging, während die Junitemperatur von 1900–1930 unablässig abnahm und zwar in einem viel stärkerem Masse als die Apriltemperatur.

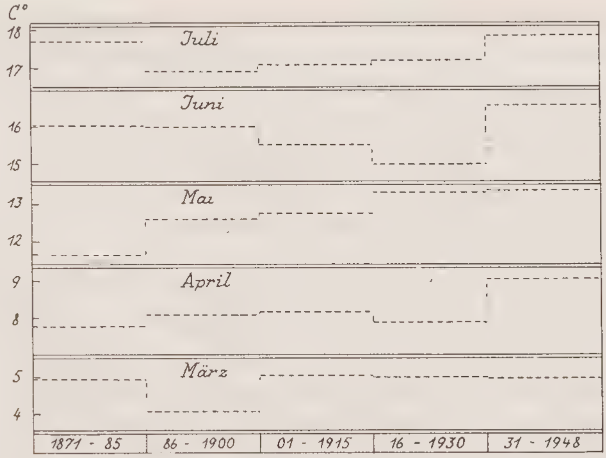


Fig. 1. Erklärung in Text.

Von 1930 ab[1] änderten sich diese Verhältnisse so, dass die Märztemperatur geringfügig sank, die Maitemperatur ungefähr gleich blieb, dagegen die April-, Juni- und Julitemperaturen sich *stark erhöhten.* Das Klima wurde kontinentaler (Klimadiagramm).

Die Klimakurve (Fig. 1) zeigt, dass die Bestandsabnahme der behandelten Arten im Zeitraum 1900–1930 mit einer Temperaturabnahme in den Monaten April und Juni, und in gleicher Weise die Zunahme dieser Arten im Zeitraum 1930–1948 einer Temperaturerhöhung in den gleichen Monaten parallel geht.

Nun handelt es sich bei den besprochenen Arten um Vögel, die in der Mehrzahl im April zurückkehren und wohl alle im Juni (und Juli, der seit 1930 ebenfalls eine Temperaturerhöhung aufweist,) Junge aufziehen. Wir glauben daher mit hoher Wahrscheinlichkeit schliessen zu dürfen, dass für die Bestandsveränderungen in der Vogelwelt des behandelten Gebietes im letzten halben Jahrhundert in erster Linie die parallel verlaufenden Klimaänderungen verantwortlich zu machen sind. Die Temperatursteigerung seit 1930 kann sich in zweifacher Weise ausgewirkt haben: Es kann eine Prolongation des Zuges von Vögeln, vor allem von Jungvögeln in die wärmer gewordenen Gebiete stattgefunden haben, und es können günstigere Aufzuchtsbedingungen geschaffen sein, sei es, dass die durch Untertemperaturen hervorgerufene Jungensterblichkeit herabgesetzt ist, sei es, dass günstigere Ernährungsmöglichkeiten (Insektenfresser) geschaffen wurden, teilweise könnten auch die Zweitbruten vermehrt worden sein. Es kann der eine Faktor allein, es können auch beide Faktoren zusammen gewirkt haben, im letzteren Falle dürfte die Zunahme besonders stark sein. Das Klimadiagramm spricht wohl dafür, dass der Juni (mit Juli) der entscheidende Monat gewesen ist. Das gleiche gilt im umgekehrten Sinne für die vorhergehende Periode. Bei sehr klimaempfindlichen Arten muss sich schon ein Jahr im günstigen oder ungünstigen Sinne auswirken. Tatsächlich konnten solche Jahresschwankungen im Bestand einzelner Arten festgestellt werden. Allerdings konnte nicht bei allen wärmebedürftigen Arten eine positive Reaktion auf die jüngste Temperaturerhöhung beobachtet werden (*Sylvia*-Arten, *Hippolais*), und *Serinus canaria* breitete sich sogar während der ungünstigen Periode aus, einige der genannten Arten vermehrten sich schnell, andere langsam. Hierin kommt offenbar zum Ausdruck, dass jede Art sich im Grunde individuell verhält und nicht nur durch diese Faktoren, sondern auch durch eine Anzahl weiterer in ihrer Bestandsentwicklung beeinflusst wird. Man denke z. B. an die Wirkung der strengen Winter auf *Galerida cristata*, die günstige Brutergebnisse wieder zunichte machen konnte. Das Klima ist nur ein Faktor der Bestandsregelung unter vielen, aber — dafür sprechen diese Beobachtungen — ein sehr wichtiger.

---

[1] Für die Mitteilung der Temperaturwerte sei dem Leiter der Münsterschen Wetterwarte, Herrn Dr. Janssen auch an dieser Stelle bestens gedankt.

Zum Schluss einige Folgerungen und Anregungen:

Die bisherige Annahme, dass die menschlichen Eingriffe in erster Linie schuld seien an der Abnahme oder dem Verschwinden unserer wärmebedürftigen Arten, muss als erschüttert gelten. Trotz weiter fortgeschrittener Kultivierungsarbeiten nehmen diese Arten in dem behandelten Gebiet wieder zu, wenn nötig sogar unter ökologischer Umstellung (vergl. *Columba oenas*).

Durch gewissenhafte Beobachtung von Klima — und Bestandsschwankungen kann und sollte der Ansatzpunkt der Klimaempfindlichkeit bei den verschiedenen Arten festgestellt werden (Zug? Brut? Jungenaufzucht?)

Die Reaktion auf Klimaänderungen erfolgt bei einigen Arten sehr schnell, bei anderen langsam. Hierüber sollten ebenfalls genaue Beobachtungen angestellt werden. (Fragen: Zugprolongation? Höhere Aufzuchtsziffern? Vermehrte Zweitbruten? Entgegengesetzt wirkende Faktoren, usw.)

Hingewiesen sei schliesslich auf die Bedeutung langfristiger Klimaschwankungen für die Züchtung angepasster Populationen in klimatischen Grenzgebieten. (Die besprochenen Arten sind offenbar alle über ihre optimalen Gebiete hinaus vorgestossen.) Hier kann in Verbindung mit Populationsdruck und Ortstreue die Klimaschwankung Individuen auslesen, die durch Kühle — oder Wärmeresistenz, Verlegung der Brutzeit, Verkürzung der Fortpflanzungszeit usw. einheitliche Populationen bilden, die als Pioniere weiter vorstossen und das Ausgangsmaterial geographischer Rassenbildung sein können.

## Literaturverzeichnis

BRUNS, H., 1948. Der Berglaubsänger (*Phylloscopus bonelli* Vieill.) bei Braunlage im Harz. Orn. Ber.

GOETHE, F., 1948. Vogelwelt und Vogelleben im Teutoburgerwaldgebiet. Detmold-Hiddesen.

KALELA, O., 1946. Zur Charakterisierung der neuzeitlichen Veränderungen in der Vogelfauna Mittel- und Nordeuropas. Ornis Fennica XXIII. (Daselbst die weiteren Arbeiten des Verf.)

KOCH, R., 1924. Veränderungen in der Ornis des Münsterlandes innerhalb der letzten 60 Jahre. 50–52. Jahresber. Zool. Sekt. Westf. Prov. Ver. f. Wissensch. und Kunst. Münster (O. J. [1924]).

KUHLMANN, H., 1950. Die Vogelwelt des Ravensberger Landes und der Senne. 11. Jahresbericht Natw. Ver. Bielefeld und Umg.

LANDOIS, H., 1886. Westfalens Tierleben II. Paderborn und Münster.

RINGLEB, F., 1940. Klimaschwankungen in Nordwestdeutschland. (Seit 1835.) Arbeiten der geogr. Kom. im Prov. Institut für westf. Landes- u. Volkskunde. Münster.

SÖDING, K., 1950. Stelzenläufer in Westfalen. Orn. Mitt. (und briefl.)

TIETGE, R., 1949. Die Blauracke ist wieder Brutvogel im Kreise Gifhorn. Beitr. z. Natk. Nieders. Nr. 8.

WILLKE, O., 1949. Blauracken brüteten in der Südheide. Beitr. z. Natk. Nieders. Nr. 8.

# Der Einfluss der letzten Wärmeperiode (1930–49) auf die Vogelfauna Nordfinnlands

*Einari Merikallio*

*Kerava, Finnland*

Wie bekannt, ist während der letzten Jahrzehnte sowie in den nordischen Ländern als auch in Finnland eine über das Normale hinaufteigende Temperatur festgestellt worden. Fig. 1 zeigt die Beobachtungen, die in den Jahren 1831–1948 in Helsinki gemacht wurden. Für den Einfluss dieser erhöhten Temperaturen auf sowohl die Tierwelt als auch auf das Pflanzenreich sind mehrere Beispiele angeführt worden. In Finnland ist eine Zunahme der südlichen, dagegen aber eine Abnahme der nördlichen Vogelarten konstatiert worden. Wir haben auch auf Grund einer quantitativen Statistik nachweisen können, dass sich innerhalb eines zwischen dem ehemaligen Grenzkarelien und Ostkarelien gelegenen Gebietes in den Quadraten E/14, F/13 und F/14 (vgl. Fig. 3) im Vogelbestande der Anteil des nördlichen Vogelelementes während der Jahre 1919 bis 1943 an der Gesamtmenge der südlichen und nördlichen Arten von 29,6 % auf 14,4 % vermindert hatte.[1]

Fig. 2 zeigt, dass auch in Nordfinnland, insbesondere während der 1930-er Jahre, in den Monaten Mai–Juli ein bedeutendes Steigen der Temperatur stattgefunden hat. Da wir einerseits eine quantitative Statistik besitzen, die mit Hilfe von Linientaxierungen (vergl. die Zahlen Fig. 3 und 4) aufgestellt worden ist[2], und uns andererseits auch ein älteres, in den Jahren 1910 –1929 gesammeltes Material zur Verfügung stand, hat sich uns Gelegenhiet geboten, auf Grund dieser Statistiken die Einflüsse der letzten Wärmeperiode auf die Vogelfauna Nordfinnlands zu klären. Hier beschränken wir uns hauptsächlich darauf, die Veränderungen zu beleuchten, welche sich in der Anzahl und Verbreitung zweier Vogelarten, nämlich des Buchfinken

[1] Merikallio, E., 1946, Über regionale Anzahl und Verbreitung der Vögel in Süd- und Mittelfinnland, besonders in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen. 1. Allgemeiner Teil. — Ann. Zool. Soc. Zool. Bot. Fenn. Vanamo, 12, n:o 1, p. 1–141.

[2] Die Untersuchungsmethode ist im Op. cit. näher erklärt worden. Die Länge der gezogenen Linie ist 580 km. Auf dieser Strecke wurden insgesamt 16 794 Vogelpaare angetroffen.

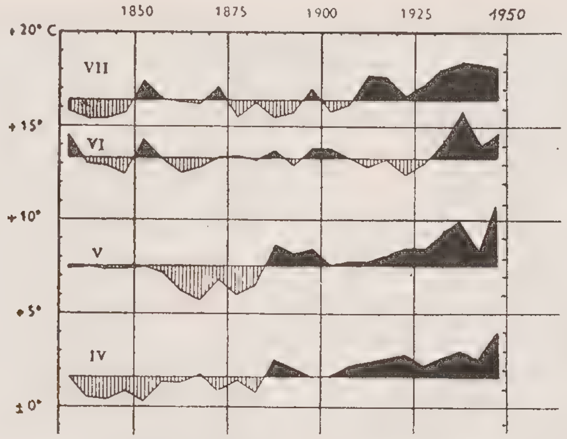


Fig. 1. Die Temperaturentwicklung des Frühjahrs und des Sommers von 1831–1948 in Helsinki.
The diagram shows the temperatures at Helsinki in the years 1831–1948.

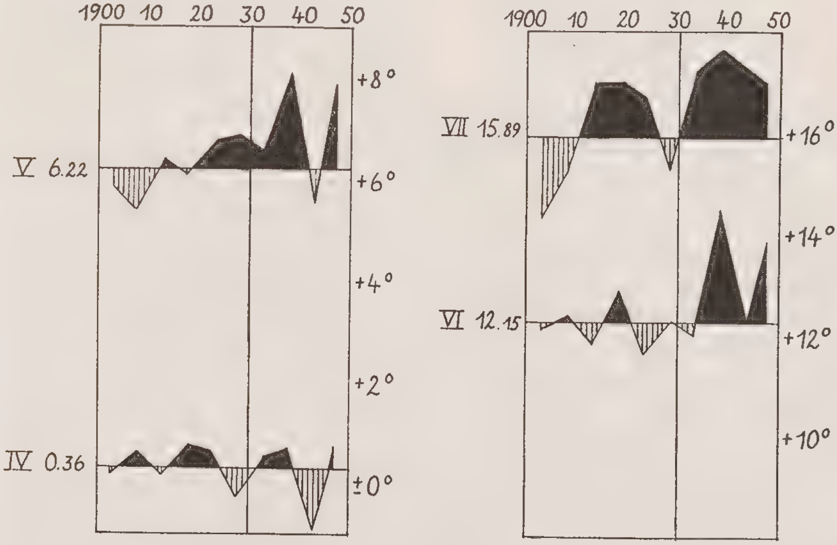


Fig. 2. Die Temperaturentwicklung des Frühjahrs und des Sommers seit 1900 in Oulu (Uleåborg), Nordfinnland.

The diagram shows the temperatures at Oulu (Uleåborg) in the years 1900–1948. As regards the Aprils, no increase in warmth can be observed after 1930, but on the contrary there is an enormous rise in temperature in other months, which reaches its climax at the end of the 1930's, to fall again in the beginning of the 1940's and to rise again nearly as high at the end of the same decade.

**Tabelle 1. Die allgemeinsten Vogelarten in Finnland nach Linientaxierungen in J. 1941–49.**

| | | | |
|---|---|---|---|
| 1. | Phylloscopus trochilus | 7 690 000 | Paare |
| 2. | *Fringilla coelebs* | 6 680 000 | |
| 3. | Anthus trivialis | 2 190 000 | |
| 4. | *Parus atricapillus* | 2 040 000 | |
| 5. | Emberiza citrinella | 1 390 000 | |
| 6. | Muscicapa striata | 1 110 000 | |
| 7. | Sylvia borin | 1 000 000 | |
| 8. | *Parus cristatus* | 960 000 | |
| 9. | Phoenicurus phoenicurus | 810 000 | |
| 10. | Turdus ericetorum | 700 000 | |
| 11. | Loxia curvirostra | 650 000 | |
| 12. | *Regulus regulus* | 580 000 | |
| 13. | Phylloscopus collybita | 550 000 | |
| 14. | Saxicola rubetra | 520 000 | |
| 15. | Erithacus rubecula | 520 000 | |
| 16. | Emberiza rustica | 490 000 | |
| 17. | Carduelis spinus | 490 000 | |
| 18. | Turdus musicus | 480 000 | |
| 19. | Lyrurus tetrix | 470 000 | |
| 20. | Tetrastes bonasia | 470 000 | |
| 22. | *Parus major* | 410 000 | |
| 26. | *Fringilla montifringilla* | 370 000 | |
| 32. | *Parus cinctus* | 280 000 | |
| 60. | *Parus ater* | 30 000 | |
| | Zus. | 37 780 000 | Paare |

The list shows the numbers of the most common Finnish birds, based on quantitative surveys carried out in 1941–49. In this list have been included the 20 most common species, and in addition 4 rarer species the numbers of which are dealt with in this paper. The names of these, as well as of other species treated in this paper, are given in italics. As we see, the willow warbler and the chaffinch are overwhelmingly predominant compared with the other species. The total number of individuals in the whole Finnish land bird fauna is estimated as 37 780 000 pairs.

(*Fringilla coelebs*) und des Bergfinken (*Fringilla montifringilla*) vollzogen haben. Die Anzahl dieser Arten geht aus folgender Statistik über die allgemeinsten Landvogelarten Finnlands hervor (Tabelle 1).

Fig. 3 A zeigt die Mengenverhältnisse der obenerwähnten zwei Arten in den untersuchten Quadraten in den Jahren 1941–49. Die Zahlen über dem Strich zeigen die Anzahl der angetroffenen Bergfinkenpaare, die Zahlen unter dem Strich diejenige der Buchfinkenpaare. Die quer durch die Karte laufende ausgezogene Linie zeigt die Stellen, wo die beiden Arten in gleicher Anzahl vertreten sind. Die am rechten Rande der Figur be-

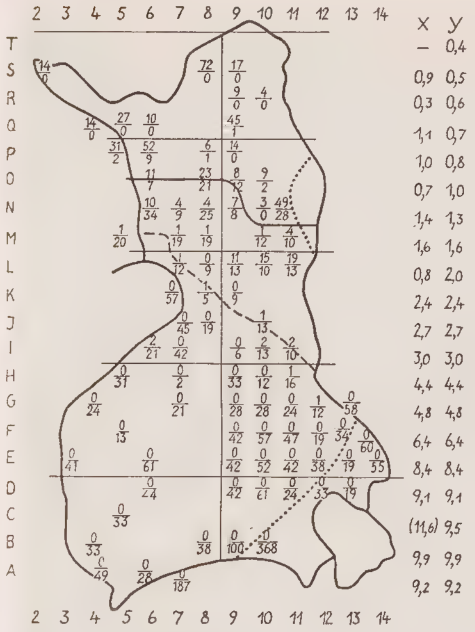


Fig. 3 A.

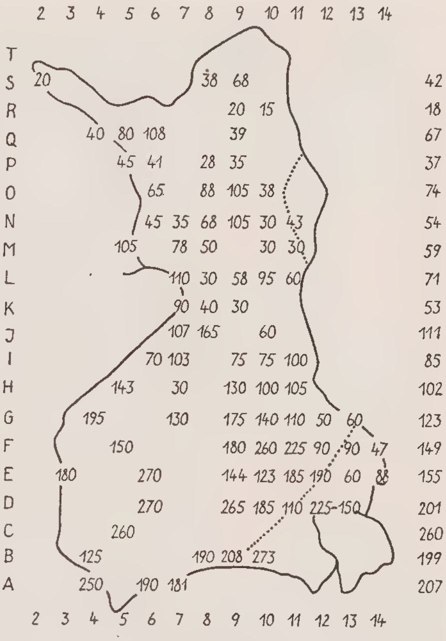


Fig. 3 B.

Fig. 3 A. Resultate der quantitativen Untersuchungen über *Fringilla montifringilla* / *Fringilla coelebs* in Finnland von 1941–49.

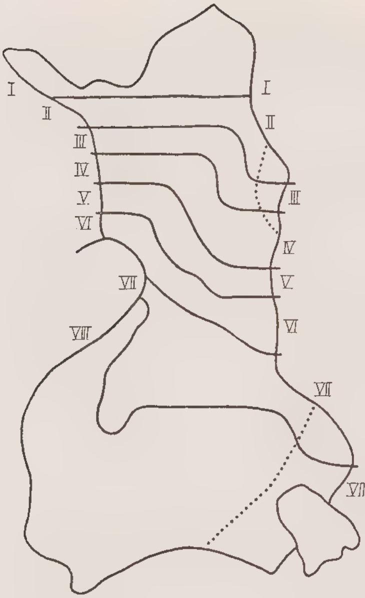
The map shows the relative numbers of *Fringilla montifringilla* and *F. colebs* in Finland according to the results of the line survey in 1941–49. The numbers of pairs obtained within the auditory belt from all the transects in each square have been presented so that at each site the numbers of *F. montifringilla* are above the line and those of *F. coelebs* below it. In South Finland only noughts are found above the line, showing the absence of *F. montifringilla*. Not until square G 12 does *F. montifringilla* appear for the first time, and not until the rows of squares O–N does it surpass the chaffinch. The vertical column X shows the number of pairs of the two *Fringillae* in each row of squares along a line on an average 4 km long, within the main belt, *i.e.* on an area of 1/5 sq. km. The numbers are seen to decrease fairly regularly towards the north, indicating a deterioration in living conditions. Since biotope checkings have not been made in the rows of squares, irregularities are caused in the number column. In the vertical column Y attempts have been made to eliminate the irregularities. The number for row C is given in brackets because it is based on one transect only.

The main boundary between the two species in 1941–49 is drawn in the map at the level of rows O–N (full line). The corresponding boundary according to the quantitative statistics of 1910–1921 ran much lower and is represented in the map by a broken line, showing that the main boundary between these species has moved in the west about 110 km, and in the east about 260 km northwards.

The dotted lines in Fig. 3–6 indicate the boundary upon Russia after 1940.

Fig. 3 B. Die Vogeldichten (Paare/km²) der Untersuchungspunkte nach den Linientaxierungen von 1941–49.

The map shows the density (pairs/sq. km) of the land bird fauna in Finland according to the transects of 1941–49, given according to square. The vertical column on the right shows these values for each row. The numbers in the vertical column increase fairly evenly towards the south and at the same time coincide with the growth of the Finnish forests, thus showing that both are dependent on the general productive capacity of the soil.



| | 1910-29 | | 1941-49 | |
|---|---|---|---|---|
| I | | | $\frac{116}{0}$ | 0,0% |
| II | $\frac{310}{2}$ | 0,7% | $\frac{96}{1}$ | 1,0% |
| III | $\frac{934}{67}$ | 6,7% | $\frac{164}{42}$ | 20,4% |
| IV | $\frac{442}{120}$ | 21,4% | $\frac{88}{93}$ | 51,4% |
| V | $\frac{124}{68}$ | 35,1% | $\frac{30}{109}$ | 78,4% |
| VI | $\frac{286}{339}$ | 54,2% | $\frac{7}{88}$ | 92,6% |
| VII | $\frac{96}{1249}$ | 92,9% | $\frac{4}{539}$ | 99,9% |
| VIII | $\frac{5}{874}$ | 99,4% | $\frac{2}{1364}$ | 99,9% |

Fig. 4. *Fringilla montifringilla / Fr. coelebs.* Die regionalen Quantitätszonen in Finnland von 1941–49.

On the map zones are shown, beginning from the western frontier of Finland, in which the ratio of the species in question is the same. The figures in the right margin indicate the number of pairs found in each zone, the figure above the line giving the number of *Fringilla montifringilla*, and the figure below the line giving the number of *Fringilla coelebs*, separately in 1910–29 and 1941–49. The same ratio is represented by the percentages, giving the proportion of chaffinches in the total of the two species. The statistics show a great shift of the main boundary of these species northwards. The numbers of the chaffinch in Finland have increased by 4.7 per cent, and those of *Fringilla montifringilla* decreased by 44.8 per cent, *i.e.* by about a half.

findlichen Zahlenreihen scheinen durch das gleichmässige Sinken ihrer Ziffern zu beweisen, dass die genannten Finkenarten konkurrierende Arten sind. Das Abnehmen der Ziffern nach Norden hin — ebenso wie auch das Sinken der allgemeinen Vogeldichte (vgl. Fig. 3 B) deckt sich mit dem abnehmenden Zuwachs der Wälder in gleicher Richtung. Die Dichte des Vogelbestandes, ebenso wie die gemeinsame Dichte der Finken, steht demnach im engsten Zusammenhang mit der biologischen Produktionsfähigkeit des Erdbodens.

Eine ähnliche Untersuchung wurde schon in den Jahren 1910–21 ausgeführt. Die Linie, längs welcher die beiden Arten damals in gleicher Anzahl vertreten waren, ist in Fig. 3 A gestrichelt eingezeichnet worden. Es ist aus der Fig. 3 A ersichtlich, dass sich die fragliche Linie in der Zeitspanne von 1910–21 bis 1941–49 an der Westgrenze des Landes um etwa 110 km und an der Ostgrenze um etwa 260 km nach Norden verschoben hat.

Auf Fig. 4 ist Finnland in Zonen eingeteilt, in welchen die Mengenverhältnisse der beiden Arten konstant sind (siehe Bilderklärung). Die am rechten Rande befindlichen Zahlen verdeutlichen die Grösse der eingetretenen Veränderung von 1910–29 bis 1941–49. Eine nähere Erklärung befindet sich unter dem Bilde.

Wir kommen also zu dem Gesamtergebnis, dass sich seit dem Jahre 1929 in ganz Finnland bezüglich der Verbreitung des Buchfinken und des Bergfinken eine bedeutende Verschiebung feststellen lässt, indem das Verbreitungsgebiet des Buchfinken sich stark vergrössert hat, während dasjenige des Bergfinken sich entsprechend verminderte. Die Zone, innerhalb welcher beide Arten gleich stark vertreten waren, ist um etwa zwei Breitengrade nach Norden und Nordosten gerückt.

Wie hat sich nun die hier geschilderte Veränderung auf die Anzahl der beiden Vogelarten in ganz Finnland ausgewirkt?

Wie bereits erwähnt (Tabelle 1), betrug die Anzahl der Buchfinken in Finnland gemäss den Ergebnissen der quantitativen Untersuchungen in den 1940-er Jahren 6 680 000 Paare und diejenige der Bergfinken 370 000 Paare, oder insgesamt 7 050 000 Paare. Es scheint dass, ungeachtet der Verschiebungen der beiden Arten, die Gesamtquantität sich nicht nennenswert verändert hat. Wir können nämlich die Anzahl jeder der beiden Arten vor 1930 und ebenso auch ihre Gesamtanzahl innerhalb eines jeden Quadrats nach dem Machtverhältnis, das in den Jahren 1910–1929 zwischen den Arten bestanden hat, berechnen. Wenn wir dann für alle Quadrate die nämliche Ausrechnung vornehmen, wobei wir bei denjenigen von ihnen, in denen die Ausführung von Untersuchungen in bezug auf eine der beiden Wärmeperioden, oder sogar auch auf beide, unterblieben ist, den Durchschnittswert der Zone einsetzen, so ergibt sich dass es in den Jahren 1910–29 in Finnland 6 380 000 Buchfinkenpaare und 670 000 Bergfinkenpaare gegeben hat. Die Anzahl der Buchfinken ist somit wahrscheinlich um ung. 300 000 Paare oder um 4,7 % gestiegen, diejenige der Bergfinken dagegen um ebensoviele Paare, oder um 44,8 %, gesunken.

Ebenso wie bei den Finkenarten haben wir auch bei anderen Vögeln ganz ähnliche Veränderungen in der Verbreitung und Anzahl festgestellt, so z. B. bei *Parus cinctus* und *Parus cristatus* (Fig. 5 A). Zusammen mit anderen *Parus*-Arten und mit *Regulus regulus* scheinen sie eine nahrungsbiologische Einheit zu bilden. Hierfür sind die rechts neben der Karte stehenden (siehe Fig. 5 B), gleichmässig nach Norden abnehmenden Mittelwerte ein Beleg. Die gemeinsame Anzahl der genannten Arten in einer

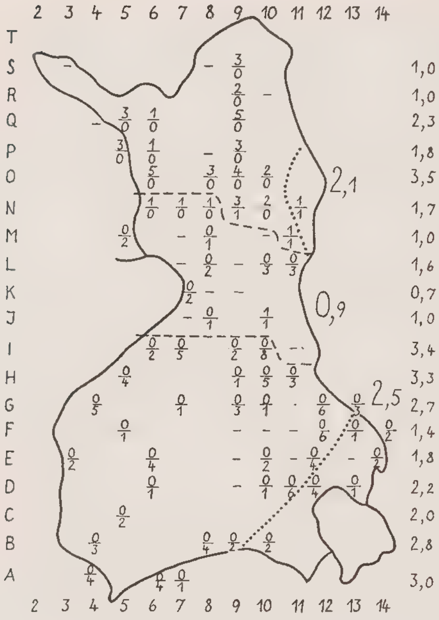


Fig. 5 A.

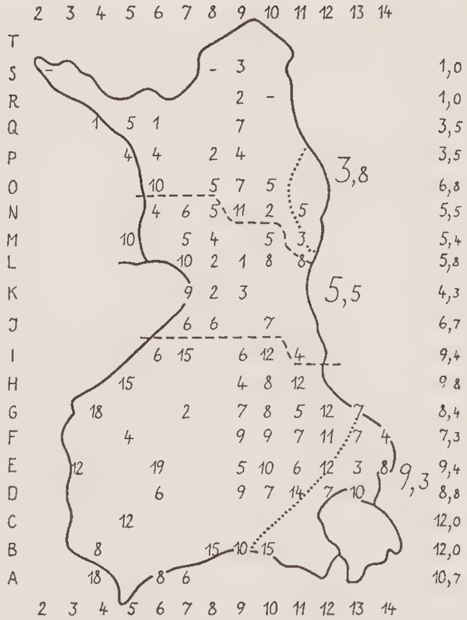


Fig. 5 B.

Fig. 5 A. Resultate der quantitativen Untersuchungen über *Parus cinctus* / *Parus cristatus* in Finnland in Jahren 1941–49.

The map shows the relative numbers of *Parus cinctus* and *P. cristatus* in Finland within the auditory belt 1941–49. The Figures are average numbers of pairs along a 4 km transect in each square. The broken lines in the middle indicate the area of Finland in which the combined number of pairs of the two species is smaller (0.9) than on either side. The species do not seem to be really vicarious, as *F. montifringilla* and *F. coelebs* are.

Fig. 5 B. Die gemeinsame Menge (Paare/4 km) der *Parus*-Arten und *Regulus regulus* nach den quantitativen Untersuchungen von 1941–49.

The map shows the combined number of pairs of all the *Parus* species and *Regulus regulus* in each square along a transect on an average 4 km long. The minimum occurring in the middle zone in the previous map—mainly due to *Parus atricapillus*—has been filled and the means of the rows in the right margin decrease from south to north fairly evenly. These species together seem to form biologically a single feeding unit.

Gegend wird von der vorhandenen Menge geeigneter Nahrung begrenzt. Da die betreffenen Arten im grossen und ganzen überwinternde Standvögel sind, dürfte die Menge der Winternahrung als derjenige Faktor anzusehen sein, der ihre Anzahl bestimmt.

Fig. 6 zeigt die Mengenverhältnisse zwischen *Parus cinctus* und *Parus cristatus* in den Jahren 1910–29 und insbesondere die Statistiken der Quadrat-

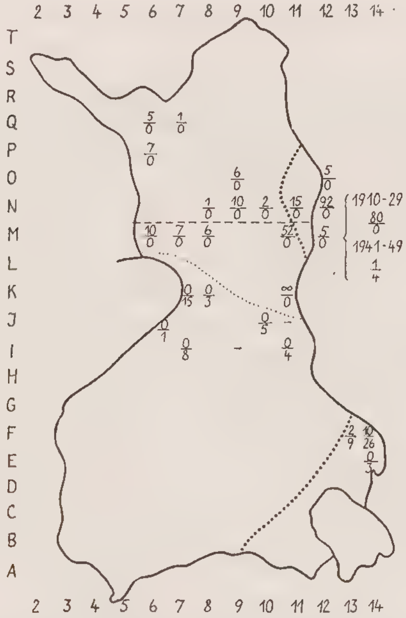


Fig. 6. Resultate der quantitativen Untersuchungen über *Parus cinctus*, *Parus cristatus* in Finnland in den Jahren 1910–29.

The figure shows the numbers of pairs of *Parus cinctus* and *Parus cristatus* in the light of older quantitative statistics in the critical zone in 1910–29. The dotted line represents the boundary between the ranges of the species 1910–29, whereas the broken line is the boundary along which the abundance relations are the same in 1941–49 (cf. Fig. 5 A). *P. cristatus* was not found at all during the years 1910–29 in the area between the lines, whereas, on the other hand, it was almost the complete possessor of this area in 1941–49, as shown by the statistics 1910–29 resp. 1941–49 (cf. Fig. 5 A). The statistics of these two periods are summarized to the right of the figure. In the west the dominance boundary had moved about 80 km, and in the east nearly 200 km towards the north.

reihe M über die verschiedenen Wärmeperioden, woraus hervorgeht, dass eine bedeutende Verschiebung nach Norden stattgefunden hat.

Wir haben hier auf der Grundlage eines quantitativen Materials ein paar Beispiele von Veränderungen vorgebracht, die sich während der letzten Jahrzehnte in Finnlands Vogelfauna vollzogen haben und die offenbar durch ein festgestelltes Wärmerwerden des Klimas verursacht worden sind. Gleichartige Phänomene sind auch im allgemeinen hinsichtlich der Verbreitung anderer südlicher und nördlicher Arten vermerkt worden, wofür aber weitere Beispiele anzuführen wir eben keine Gelegenheit haben.

*Diskussion*:

A. Hemmingsen: In einer früheren Arbeit hat Palmgren die Ansicht geäussert, dass die Ursachen, warum der Buchfink (*Fringilla coelebs*) im nördlichen Finnland nicht brütet, nicht in seiner Unfähigkeit, bei den dort herrschenden niedrigeren Temperaturen zu brüten, zu suchen ist. Vielmehr soll nach Palmgren die Ursache darin liegen, dass seine Brutinstinkte schon zu der Zeit zum Ausdruck kommen, wo er auf dem Frühlingszug nicht länger als bis ins südliche Finnland gekommen ist. Deswegen möchte ich gern fragen, ob die von Dr Merikallio beschriebenen Verschiebungen in der Ausbreitung des Buchfinken in Finnland nicht mit Änderungen der Ankunftszeit dieser Art in Finnland zusammenhängen?

E. Merikallio: In welchem Masse die Zugzeit des Buchfinken unter der Einwirkung der letzten Wärmeperiode sich verändert hat, ist bisher noch nicht klargestellt worden.

Es ist meine Absicht, mit der Behandlung der Frage, welchen Einfluss die letzte Wärmeperiode auf die Zugzeit der Vögel in Finnland ausgeübt hat, in nächster Zukunft zu beginnen.

F. Salomonsen: Die beiden *Fringilla*-Arten sind ökologisch doch so verschieden, dass sie nichs als ausgesprochene Nahrungskonkurrenten bezeichnet werden können. *F. montifringilla* ist viel mehr als *F. coelebs* an Birkenwälder gebunden und es gibt auch Verschiedenheiten in der Beziehung der beiden Arten zur Lufttemperatur (*F. coelebs* geht z. B. *nicht* in die subarktische Birkenzone hinauf, wo *F. montifringilla* immer alleinherrschend ist). Die Verschiebung der beiden Arten hat daher sicher teilweise unabhängig voneinander stattgefunden. Eine sicherer Fall von Nahrungskonkurrenz liegt m. E. in *Carduelis flammea rostrata* und *C. f. hornemanni* in Grönland vor, deren gegenseitige Grenze sich etwa 200 km in den Jahren 1920—1935 gegen Norden verschoben hat.

E. Merikallio: Meiner Erfahrung gemäss sind sowohl *Fringilla coelebs* als auch *Fringilla montifringilla* recht eurytope Arten, was durch die in Finnland gemachten Biotopuntersuchungen nachgewiesen ist. Allerdings ist an den Grenzen ihrer Verbreitungsgebiete ein Wählen der Biotope feststellbar. So ist *Fringilla coelebs* an seiner Nordgrenze ein Vogel der Flussufer und der bewohnten Gegenden, während *Fringilla montifringilla* im Süden kühle Sumpfgegenden zu bevorzugen scheint. Dieses hat jedoch an der Grenze der Vorherrschaft zwischen den beiden Arten nichts mit dem Phänomen der Nahrungskonkurrenz zu tun, denn dort sind beide Arten durchaus eurytop. Es dürfte klar sein, dass die Verschiebung der beiden Arten nach Norden hin von klimatischen Faktoren bewirkt worden ist.

M. v. Udvardy: 1) Leben die beiden Finkarten in Mittelfinnland in denselben Biotopen?

2) Wenn sie dass tun, konnte man feststellen, ob sich in irgendeinem Fall die Reviere der Beiden einander völlig oder teilweise decken?

3) Gibt es direkte Konkurrenz zwischen der ♂♂ der Beiden; zeigt der Buchfink ♂ Agressivität gegen den Bergfink ♂?

E. Merikallio: 1) Siehe, was bereits vorher über die Biotope der Arten erwähnt wurde.

2) Eigentliche Revieruntersuchungen sind nicht vorgenommen worden, doch gelegentliche Beobachtungen weisen darauf hin, dass die Reviere der betreffenden Arten einander nicht decken. Diese Ansicht wird unterstützt von den Untersuchungsergebnissen über die Verbreitung der gemeinsamen Anzahl beider Arten.

3) Direkte Beobachtungen liegen nicht vor.

# On the Recent Fluctuations in Numbers of Waterfowl in the Finnish Archipelago

*Pekka Grenquist*

*Helsinki*

As a consequence of the latest decline in the waterfowl populations, it became necessary to treat the waterfowl question in Finland from a quantitative point of view. The Game Research Institute in Helsinki organized in the summer of 1947 a network for waterfowl observation in the Finnish Archipelago, and a year later annual census-work was started at so-called control stations in different parts of the Archipelago. Statistics have been collected and compared with the scarce statistical data from the 1930s and the early 1940s.

I shall try to give a preliminary survey of the fluctuations in the breeding populations of the diving ducks, the surface feeding ducks, the sawbills and the grey lag goose in the Finnish Archipelago during the last two decades. The numerous birds are treated first.

The Eider Duck (*Somateria mollissima* L.) increased during the 1920s and reached a maximum in the spring of 1930. The breeding season of 1931 was distinguished by a decline and an epidemic (Forsius 1932) among the young and the females. But already in the year 1933 the population was as dense as three years earlier. A new maximum, bigger than before, was reached either in 1933 or 1934, or probably as late as in early spring 1935. This year was the beginning of a long decline, the details of which are difficult to follow because of the war. A few weeks after the young had hatched in the summer of 1935 a violent epidemic, caused by *Polymorphus boschadis*, arose (Lönnberg 1936). The epidemic among the young and females continued in 1936, 1937 and 1938 in the whole South Western Archipelago but did not make as great havoc in the latter years as in 1935. It was thought that the breeding population was reduced to about 2/3 (Lampio 1946). In Klåvskär in the Åland Archipelago the population decreased from 100 % in 1930 and 1935, to 72 % in 1939 and 36 % in 1940.

In the Kobba Klintar sanctuary the population in 1945 was only 26 %

The breeding population of eider duck in four bird sanctuaries in Åland given as a percentage of the maximum in 1930 (= 100 %).

| | 1927 | 1928 | 1929 | 1930 | 1931 | 1932 | 1933 | 1934 | 1935 |
|---|---|---|---|---|---|---|---|---|---|
| Klåvskär........................ | 87 | 83 | 94 | 100 | — | 88 | 96 | 99 | 100 |
| Kobba Klintar (Nordberg 1951) ... | 60 | 66 | 76 | 100 | 78 | 133 | 118 | 120 | — |
| Signilskär (Nordberg 1951)........ | — | — | 99 | 100 | 95 | 96 | 101 | 108 | — |
| Lågskär ,, ,, ........ | 56 | 63 | 76 | 100 | — | 92 | 116 | — | — |
| Total.. | — | — | 92 | 100 | — | 92 | 101 | — | — |
| Total breeding pairs.. | — | — | 2908 | 3171 | — | 2929 | 3214 | — | — |

of the population in the year 1930 and the total number in Klåvskär, Signilskär and Lågskär in 1949 only 46 % of the population in the year 1930. This decline of more than 50 % in 19 years is not significant for the total Eider population in Finland. The above-mentioned bird sanctuaries were almost the only areas in the Åland Archipelago, where the eider ducks were under total protection in the 1930s. Now nearly 1/4 of the whole Archipelago is under protection (Nordberg 1951), and the eider ducks are more equally spread over the whole Archipelago.

Since 1947 an increase in the total population all over the Finnish breeding ranges has been observed. In some outlying parts of the breeding range the population is already on a level with the population in the summer of 1930. In a few sanctuaries east of Helsingfors the number of breeding pairs is even higher than in 1930.

The Velvet Scoter (*Melanitta fusca* L.) does not breed in great numbers in the outer skerries, where the census of the species was made in the 1930s. In many parts of the outer Archipelago the velvet Scoter is a late resident. There are islets with the first breeding pairs in the 1920s, 1930s, and 1940s. Quite a great increase in the number of breeding birds was noted in the middle of the 1930s. The species has also increased in the 1940s. This increase in the population has been considerable in the years 1947, 1948 and 1949. In the Archipelago there are many areas, where the breeding population is now more numerous than in the year 1930. The observations indicate that the velvet scoter has increased all over the Finnish Archipelago in the last decades.

The Goosander (*Mergus merganser* L.) and the Red-breasted Merganser (*Mergus serrator* L.) have not shown any pronounced tendency to increase or decrease in the Archipelago. The populations of both in the south western parts of the Archipelago are about the same as in the year 1930. The goosander and the red-breasted merganser are now more numerous in the northern parts of the Gulf of Bothnia than 19 years ago and the latter in the eastern parts of the Gulf of Finland as well.

The Tufted Duck's (*Aythya fuligula* L.) tendency either to increase or decrease as a resident in the outer skerries is much the same as a reflection of the fluctuations in number in the breeding populations in the lakes and inlets of the mainland. The "expansion" to the Archipelago was remarkable in the middle of the 1930s. During these years many islets got their first breeding population of tufted ducks. Where the birds had been resident for a long time the population was increasing. Apparently in 1939–1940 a complete change occurred with a very severe decline, which continued until 1946 or 1947. During these years the bird has either disappeared from the treeless little islets or the population has declined to an almost non existent minimum. In the summer of 1948 or 1949 the decline appears to have ceased.

The Scaup Duck (*Aythya marila* L.) was an uncommon resident in the Western Archipelago from Tornio in the north to the northern islets of Åland twenty years ago. Now the bird has disappeared from Åland, and the breeding population in Kvarken in the Gulf of Bothnia is about 50 % of the population 20 years ago.

The Goldeneye (*Bucephala clangula* L.) has decreased in the Archipelago since the 1930s. No reliable signs of a turn for the better have yet been seen.

The Surface Feeding Ducks have never been numerous in the outward treeless skerries. The Mallard (*Anas platyrhyncha* L.) has decreased since the 1930s. The Teal (*Anas crecca* L.) and the Pintail (*Anas acuta* L.) are both as numerous as they were about 20 years ago. The Shoveler (*Spatula clypeata* L.), which appeared as a new breeding bird in many treeless islets in the 1930s, disappeared in the early 1940s and reappeared in the late 1940s.

The Grey Lag Goose (*Anser anser* L.) has decreased both in the 1930s and the 1940s. No increase in the very rare grey lag goose populations has yet been observed in spite of total protection since 1947.

## References

Forsius, R., 1931–32. Stor dödlighet hos sjöfågel i Föglö skärgård våren och sommaren 1931. Mem. Soc. pro F. et Fl. Fenn. 8.

Lampio, T., 1946. Riistantaudit Suomessa vv. 1924–43. Summary: Game diseases in Finland 1924—43. Suomen Riista 1.

Lönnberg, E., 1935–36. En gåtfull sjukdom på ejder i Finland. Svenska Jägareförbundets årsskrift 1935–36.

Nordberg, S., 1951. Det jaktbara villebrådet och jaktvården på Åland. Suomen Riista 6. in print.

# Spring Weather and Population Fluctuations

*Gunnar Svärdson* and *Sigfrid Durango*

*Institute of Freshwater Research, Drottningholm, Sweden*

*Täby, Sweden*

The knowledge of the present change in climate of the world has recently been summarized by Ahlmann (1949) and an extensive bibliography on the subject has also been compiled by Lee and Tåning (1949).

In Sweden this climatic change has had a marked influence on the bird fauna. Among the resident birds some northern species, i. a. *Cractes infaustus, Pinicola enucleator* and *Parus cinctus* have decreased and disappeared from the southernmost parts of their breeding area. Some southern species, however, have increased and spread to the north, i. a. *Garrulus glandarius, Chloris chloris, Parus caeruleus, P. ater* and *P. cristatus.* More birds than before have wintered in Sweden including some partial migrants, i. a. *Corvus cornix, Corvus monedula* and *Turdus merula.*

True migrants have also been affected. Quite a number of species, formerly not belonging to the Swedish fauna, have been added to the Swedish list or occurred more often than before during the nineteen thirties and forties. A short list of the more remarkable species runs like this: *Oriolus oriolus* (first nest in 1932), *Serinus canaria* (first nest 1942), *Carpodacus erythrinus* (first nest 1938), *Muscicapa parva* (first nest 1944), *Phylloscopus trochiloides* (first specimen 1939), *Locustella fluviatilis* (first specimen 1937), *Locustella luscinioides* (first specimen 1947), *Locustella naevia* (first nest 1929), *Acrocephalus paludicola* (first spring specimen 1942), *Luscinia svecica cyanecula* (first specimen 1943), *Athene noctua* (first nest 1939), *Otus scops* (first specimen 1943), *Aquila heliaca* (first specimen 1933), *Egretta garzetta* (first specimen 1949), *Netta rufina* (first specimen 1937), *Streptopelia turtur* (now seen every year, formerly vagrant; no nest), *Xenus cinereus* (first specimen 1934), *Charadrius leschenaultii* (first specimen 1938), *Himantopus himantopus* (first specimen 1944), *Anthropoides virgo* (third specimen 1934 and fourth 1947), *Gelochelidon nilotica* (second specimen 1940), and *Sterna dougallii* (first specimen 1949).

Rare birds, of course, attract the interest of Swedish amateur ornithologists more than an increase in population of more common species. No doubt, therefore, many species have increased in Sweden during the last 20 years, without being noticed in the literature. Some of them, however, are still so rare that the interest is intense. Therefore, an increase in population is definitely proved for i. a. *Motacilla cinerea, Acrocephalus arundinaceus, A. scirpaceus, A. palustris, Phoenicurus ochruros, Luscinia luscinia* and *Alcedo atthis.* A remarkable increase in population is also proved for the eutrophic lake fauna, i. a. *Cygnos olor, Aythya ferina, A. fuligula, Podiceps cristatus, Larus ridibundus, Rallus aquaticus* and *Gallinula chloropus,* though this increase is older and began already in the eighteen eighties. Some birds have been extinct as breeders in Sweden but reappeared in the thirties, i. a. *Coracias garrulus* (now about 10 breeding pairs on Gotland) and *Recurvirostra avosetta* (now about 200 pairs in Scania and on Öland).

This short survey of faunistic changes within the last decades in Sweden may serve as evidence that the bird fauna of Sweden has undergone at least as great changes as that of the other northern countries, from which more data has been published.

The purpose of this paper is to indicate how at least some of these changes in population are correlated with the climatic change. We have concentrated on a few years during the forties. For 1943, 1947, 1948 and 1949 we have compiled a table, including the species of which there was a general increase in the Swedish population, exceptional northern breeding or exceptional northern observation of scattered birds. Five birds from these years which are new to the Swedish list, have already been mentioned in the introduction, 2 from 1943, 1 from 1947 and 2 from 1949. The detailed information, on which table 1 is constructed, cannot be given here owing to lack of space. Some of the data are published in Swedish ornithological journals, some observations were reported to the authors by various correspondents and some are original.

From official meteorological sources we have also constructed the diagrams (fig. 1), giving the deviation from normality in the average monthly temperature during April and May in the forties. The localities selected are Stockholm and Lund. From the diagrams it can be seen that 1943 and 1948 have had the mildest April months and 1947 and 1949 the warmest May months during the decade. It is immediately seen that the springs of the nineteen forties were on the average much warmer than normal.

Most of the birds included in table 1 are May migrants. In 1943, when not only April but also May were warm, a number of May migrants were numerous. A general correlation of temperature within large geographical

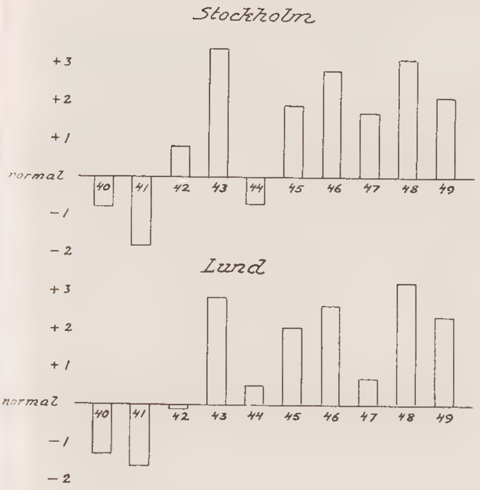


Fig. 1 A. Deviation in April from average temperature. Centigrade.

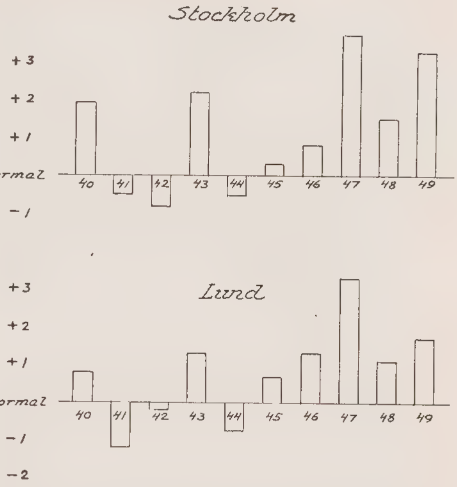


Fig. 1 B. Deviation in May from average temperature. Centigrade.

regions is often found and some of the May migrants in Sweden may also have been affected by the April weather over the Continent. In 1948, however, the first part of April especially was mild and not so many May migrants seem to have been affected. Moreover, as is now generally known, birds arriving early do not spread so fast northward as do birds arriving late.

A detailed discussion of the influence of spring weather on all the different bird species listed in table 1 cannot be permitted here. But we conclude from the data given in table 1 and the diagrams that a considerable part of the increase in population, noted in the years mentioned, was due to the extra stimulation of high temperatures during the normal migration period. This probably has principally affected birds on their first northern flight. The phenomenon is thus a mass 'prolonged migration.' We may make reference here to the experimental studies performed on caged birds and above all to the numerous field observations in all northern countries showing that migration is remarkably intensified in the warm sector of a cyclone. We think there can be no doubt that a migratory bird is stimulated by warm air to fly in the spring. Further we now know that returning to the birthplace is not nearly so strong as returning to the breeding locality of last year. Therefore population fluctuations must be principally built up by first-breeders.

The mechanism concerned may be illustrated by the bluethroat (subspecies *cyanecula*) which was observed, as the first Swedish bird of its kind,

Table 1. Bird population changes in Sweden during some recent years.

| Year | General increase | Exceptional northern breeding | Exceptional northern observation |
|---|---|---|---|
| 1943 | *Locustella naevia* | *Phylloscopus sibilatrix* | *Carpodacus erythrinus* |
| | *Luscinia luscinia* | *Upupa epops* | *Muscicapa parva* |
| | *Cuculus canorus* | *Acrocephalus scirpaceus* | *Hippolais icterina* |
| | *Asio flammeus* | *Luscinia luscinia* | *Phoenicurus ochruros* |
| | *Anas strepera* | *Numenius arquata* | *Luscinia luscinia* |
| | *Botaurus stellaris* | | *Tyto alba* |
| | *Crex crex* | | *Xenus cinereus* |
| | *Coturnix coturnix* | | *Porzana porzana* |
| | | | *Dendrocopos medius* |
| 1947 | *Lanius collurio* | *Anas querquedula* | *Phylloscopus sibilatrix* |
| | *Phylloscopus sibilatrix* | *Sterna albifrons* | *Hippolais icterina* |
| | *Sylvia nisoria* | *Jynx torquilla* | *Ciconia nigra* |
| | *Jynx torquilla* | *Coturnix coturnix* | *Podiceps nigricollis* |
| | *Anas querquedula* | *Charadrius alexandrinus* | *Chlidonias niger* |
| | *Crex crex* | | *Larus minutus* |
| | *Coturnix coturnix* | | *Upupa epops* |
| | | | *Rallus aquaticus* |
| 1948 | *Erithacus rubecula* | *Carduelis cannabina* | *Porzana pusilla* |
| 1949 | *Lanius collurio* | *Carpodacus erythrinus* | *Serinus canaria* |
| | *Hippolais icterina* | *Jynx torquilla* | *Oriolus oriolus* |
| | *Phylloscopus sibilatrix* | | *Muscicapa parva* |
| | *Motacilla cinerea* | | *Phylloscopus trochiloides* |
| | *Alcedo atthis* | | *Phoenicurus ochruros* |

at Örebro in 1943. It held a territory for some weeks but no female arrived, as could be foreseen. Next year, when spring was colder than normal, it again prolonged its migration at least 600 kilometres (from its birthplace) to reappear at Örebro in its territory from last year! The probability that two different bluethroats prolong their migration for two consecutive years at least 600 kilometres to the very same bushes is, of course, so infinitesimal as to be non-existent. The identity of the bird is thus quite certain, though it was not ringed.

If hundreds or thousands of birds react to the weather like this bluethroat a reduction of the breeding fauna might be found in the region where they were born and an increase must occur in northern regions. That the number of birds affected might sometimes be large is proved by the increase in population of *Lanius collurio* and *Anas querquedula* in 1947 when both—though they are fairly common every year—were two or three times more abundant than normal. And *Erithacus rubecula*, though it is a very common bird, doubled its number in 1948 within eastern middle Sweden, which was observed in the field and verified in a test area. Moreover, this robin invasion was also noticed in southern Finland. The garganey invasion of 1947 was noticed in Norway too and, to judge from small published reports, also in Holland and England. The invasion of *Anas strepera* in 1943 was also noticed in Schleswig-Holstein, the *Luscinia* increase of the same year in central Germany as well.

If the hypothesis, presented above, should be correct, more distributional variations of the first breeders within the European breeding area could be proved, if annual countings were made of various bird species in different localities. We are going to try to get such data from Sweden in the future. The significance for evolutionary studies of population changes of the kind mentioned goes without saying.

*Discussion:*

K. G. Wingstrand: I should like to make a remark which may also be a proof of Dr. Svärdson's interpretation. In 1943 the marsh warbler (*Acrocephalus palustris*) had decreased in Southern Sweden contrary to other birds. The temperature during its period of migration, the very last days of May, was exceptionally low.

## References

AHLMANN, H. W:SON, 1949. Introductory Address to the Meeting on Climatic Changes. Rapp. et Proc. Verb. Cons. Perm. Int. L'explor. Mère. CXXV: 9-16.
LEE, A. J. and Å. V. TÅNING, 1949. Bibliography. Ibidem: 42-52.

# The Effects of the Recent Climatic Changes on the Bird Life of Iceland

*Finnur Gudmundsson*

*Reykjavik*

It is a well known fact that a very pronounced change in climate has taken place in the northern hemisphere in recent times. It seems to have begun about the middle of the 19th century, but it has been greatly accelerated since the early years of the 20th century, and especially in the last 30 years.

The change consists first of all in a greatly increased intensity of the general atmospheric circulation, which in turn has caused a widespread amelioration of climate, most marked in higher latitudes. In arctic and subarctic regions a spectacular rise in the mean temperature of the air and the sea has occurred. It has been accompanied by a corresponding rise in precipitation and an increasing prevalence of southerly winds. Other accompanying phenomena are the shrinkage of the floating ice-cap in the Arctic, the regression of glaciers and so on.

Opinions still differ as to the principal cause of the variations in the strength of the atmospheric circulation between equator and pole, and it is beyond the scope of this paper to enter further into that matter here. But on the other hand I shall discuss briefly the trend and intensity of the climatic changes which have taken place in Iceland in recent times.

Eythorsson (1949) has recently dealt with temperature variations since the beginning of systematic meteorological observations in Iceland. On the basis of instrumental data he has been able to prove the existence in Iceland of a pronounced upward trend in temperature in the last decades. Fig. 1 and 2 illustrate this trend distinctly. Fig. 1 shows the fluctuations of the annual mean temperature of the air (and of the sea at Papey) on selected meteorological stations, as represented by 30 year moving averages. The figures by the station names are the annual means for the period 1901-1930. Graph II shows the corrected temperatures for Vestmannaeyjar, the cor-

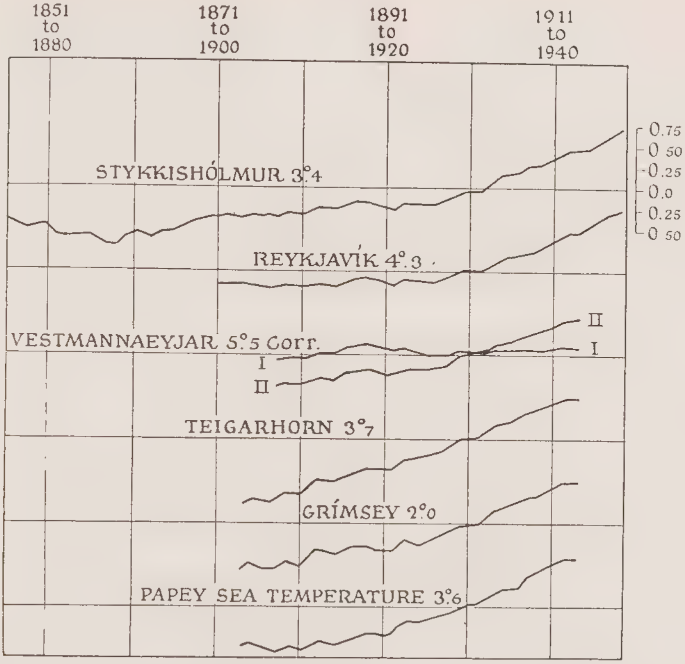


Fig. 1. Fluctuations of the annual mean temperature of the air (and of the sea at Papey), as represented by 30 year moving averages. (After Eythorsson 1949).

rection being made necessary by moving of the meteorological station in 1921 to a higher level and a more exposed place.

Fig. 2 shows the fluctuations of the monthly temperature averages at Reykjavik, as represented by 30 year moving averages. The fact that the rise in temperature has been much more pronounced in winter than in summer stands out very clearly in this figure.

In Iceland as in other arctic and subarctic regions, further distinctive features of the climatic change consist in a greatly increased prevalence of southerly winds, increased precipitation, and a rise in the temperature of the sea concordant with the rise in the temperature of the air (cf. the graph for Papey in fig. 1). A great and rapid retreat of the Icelandic glaciers and a more or less pronounced absence of pack ice from the coastal waters of Iceland since 1920 may also be mentioned as results of the above changes in the climatic factors.

All these changes in the climatic conditions, which in Iceland have been particularly pronounced and rapid after 1920, have brought about a marked amelioration of the Icelandic climate. Its consequences have been far-

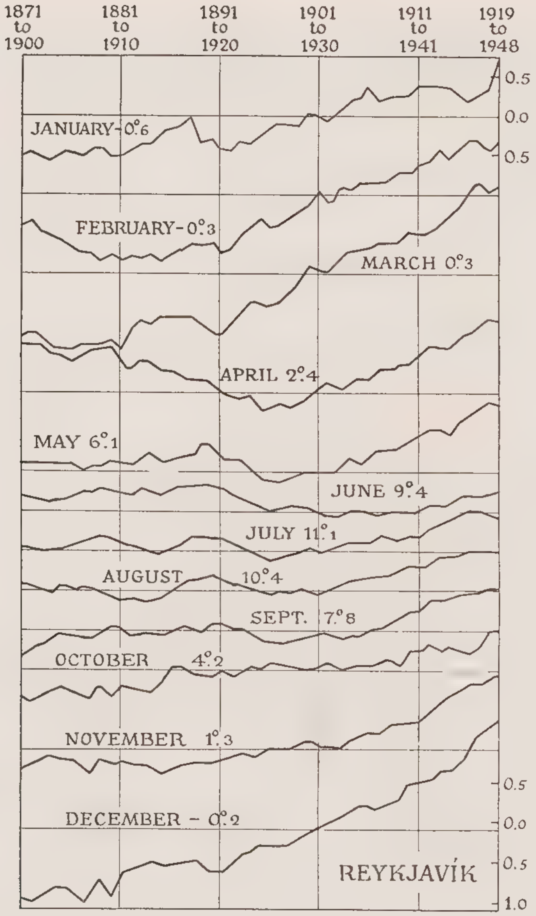


Fig. 2. Fluctuations of the mean temperature of the air for the different months at Reykjavík, as represented by 30 year moving averages. (After Eythorsson 1949).

reaching and have come to influence the everyday life of man in Iceland in many ways, and it has therefore aroused interest in wide circles of the population.

It is naturally to be expected that such great and far-reaching climatic changes as those I have outlined here should have had some effect on the fauna of Iceland, especially when we consider the geographical position of the country. Iceland lies on the boundary between the Atlantic and the Arctic Sea, its northern promontories just touching the Arctic Circle. A branch of the North Atlantic drift follows the Faroe Island ridge to the south coast of Iceland. Here it is deflected to the west, and a part of it penetrates further to the north and east coast, thus encircling the island. On the other hand, from the north cold water from the Greenland Sea penetrates to the north and east coast, where it mixes with the warm Atlantic water, sometimes carrying masses of polar ice to the coasts, especially in late winter and spring. To quote Eythorsson (1949) "the northwest coast (of Iceland) is separated from Greenland, one of the earth's main sources of cold air, by only 400 km of sea. The north coast is open to cold outbreaks from the Arctic, while the south coast faces the Atlantic with its warm surface currents and relatively warm air masses." Iceland is therefore, as it were, inserted in the Polar Front.

As a result of its position southern and arctic Fauna elements meet in Iceland. The northern limits of distribution of many southern species and the southern limits of some arctic species lie in or near the country. These species live under the more or less unfavourable conditions typical for the periphery of their respective ranges. It is therefore only natural that these species should react quickly if considerable climatic changes take place. The climatic changes that have taken place in Iceland in recent times and have been under discussion here have also been proved to have had great and far-reaching effects on the marine Fauna in Icelandic waters, but it would take us too far from the main subject of this paper to discuss that matter here. But I propose here to outline those changes in Icelandic bird life which I believe to be primarily caused by climatic changes. For the sake of convenience I shall deal with these changes under two main headings: 1. Positive changes, such as immigration, increase, or extension of range within Iceland, etc., and 2. Negative changes, such as decrease or extinction.

### *Positive changes*

The positive changes consist principally in the immigration within the last 50–60 years of no less than 7 southern species as breeding birds. These species are: The Starling (*Sturnus vulgaris* L.), the Short-eared Owl (*Asio flammeus* (Pontopp.)), the Shoveler (*Anas clypeata* L.), the Tufted Duck (*Aythya fuligula* (L.)), the Black-headed Gull (*Larus ridibundus* L.), the Herring-Gull (*Larus argentatus* Pontopp.) and the Lesser Black-backed Gull (*Larus fuscus* L.). To these should be added two southern species which have bred in Iceland for the first time in this century but have not yet become permanently established as breeding birds, namely the Swallow (*Hirundo rustica* L.) and the Coot (*Fulica atra* L.). A striking increase or extension of range within Iceland of certain old-established Icelandic breeding species with decidedly southern distribution is in my opinion also to be ascribed to the recent improvement in the climate. These species include first of all the Black-tailed Godwit (*Limosa limosa* (L.)), and also the Oyster-catcher (*Haematopus ostralegus* L.) and the Gadwall (*Anas strepera* L.).

On the other hand, the reported occurrence and even breeding of the Black-necked Grebe (*Podiceps caspicus* (Hablizl)) at Lake Mývatn in 1938 (Müller 1939) is almost certainly erroneous. It should therefore be excluded from the Icelandic List.

Other positive results of the climatic improvement are manifested in the increasing wintering in Iceland of partially migratory species and in the very noticeable increase in winter visitors, occasional visitors, and vagrants from the south.

I shall now describe these changes in detail, and shall begin with those species which have immigrated as breeding birds.

The Starling (*Sturnus vulgaris* L.) has for a long time been known as a winter visitor to Iceland, and in the last decades it may be said to have been fairly common. The first authentic breeding attempt was made in 1935 when a pair built two nests on buildings at Laugarnes just outside Reykjavik (SW.), but no eggs were laid, and the pair disappeared. But since 1941 the starling has bred in small numbers in Hornafjördur in the SE., and in 1950 a nest was found in Öræfi (Fagurhólsmýri) ca. 85 km W. of Hornafjördur. As the starlings seem here to be increasing and extending their range slowly, there is no doubt that we have here a case of permanent colonization. Two older breeding records are either erroneous (Mýrar 1912) or most likely based on a misunderstanding (Húsavik 1928).

I have not had an opportunity to examine breeding birds from Hornafjördur, but winter visitors from other parts of the country that have been examined belonged to the typical race *Sturnus vulgaris vulgaris* L.

The Short-eared Owl (*Asio flammeus* (Pontopp.)) has also for a long time been known as a winter visitor to Iceland, and it is said to have bred in S. Iceland (Hellir in Holt, Rang.) in 1912. In the years 1928 and 1929 nests were found in several places in the marshy lowlands in the counties Rangárvallasýsla and Árnessýsla in the south and in Mýrar in the west. And we know with certainty that in the years immediately preceding it had been breeding in the same districts, even if no nest finds were made. In the following years it increased very rapidly, and by now it may be said to be locally distributed as a breeding bird throughout the country.

The Shoveler (*Anas clypeata* L.) is now breeding in small numbers in three different localities in the north. Since 1931 it has been breeding at Sandur and Sílalækur in Adaldalur, since 1934 or a little later at Lake

Mývatn, and since 1937 at Arnanes in Kelduhverfi. The number of pairs in each locality is between 10 and 20. Previously it was unknown in Iceland, except that a few pairs are said to have bred at Stafholtsey in the Borgarfjördur area (W.) in 1911 and the following years, but it has not been possible to verify this information. The shoveler has also been observed in Medalland (1935) in the south, although it has not been proved to breed there, and from April to June 1939 a male shoveler paired with a female mallard stayed on the lake in the centre of Reykjavik (SW.), but it is not known if eggs were laid.

The Tufted Duck (*Aythya fuligula* (L.)) was first recorded for Iceland in 1895 when specimens were obtained on Lake Mývatn (N.). But it has increased rapidly since it was first observed. Already in the years 1904–1908 it was breeding in considerable numbers at Lake Mývatn as well as in some other localities. Since then the Tufted Duck has continued to increase steadily, at the same time extending its range within the country. After the Scaup-Duck (*Aythya marila* (L.)) it is now the second commonest duck at Lake Mývatn, and in many other parts of Iceland it now breeds commonly. It prefers lakes rich in vegetation and animal life or the eutrophic type of lake especially with some cover. Owing to its habitat preferences its distribution within Iceland is everywhere local. It is thus absent from climatically unfavourable districts, and consequently is not as extensively and evenly distributed as the Scaup-Duck.

The Black-headed Gull (*Larus ridibundus* L.) was observed in different parts of Iceland in the first decade of this century. But it was not found breeding until 1911 when at least one pair bred at Lake Thingvallavatn (SW.) and one at Eyrarbakki (SW.). In the latter place one pair bred again in the following year. After that it was hardly seen at all for a few years, but after 1920 it begins to appear more commonly again, and between 1920 and 1930 it begins to breed in a few places. Since 1930 it has been increasing rapidly and now it is breeding in small colonies in many parts of the country. In Iceland the Black-headed Gull is partly resident and partly migratory. Ringed birds have been recovered in the British Isles (3), Portugal (1), SW. Greenland (1) and Newfoundland (2). A great many, however, are wintering in Iceland, especially in the climatically favourable Southwest. Around Reykjavik, for instance, it is now the commonest Gull in winter. The unexpected recoveries in SW. Greenland and Newfoundland indicate that the Black-headed Gull will not stop at Iceland but will penetrate farther westwards and perhaps establish itself in Greenland and NE America.

The Herring-Gull (*Larus argentatus* Pontopp.) commenced to breed in

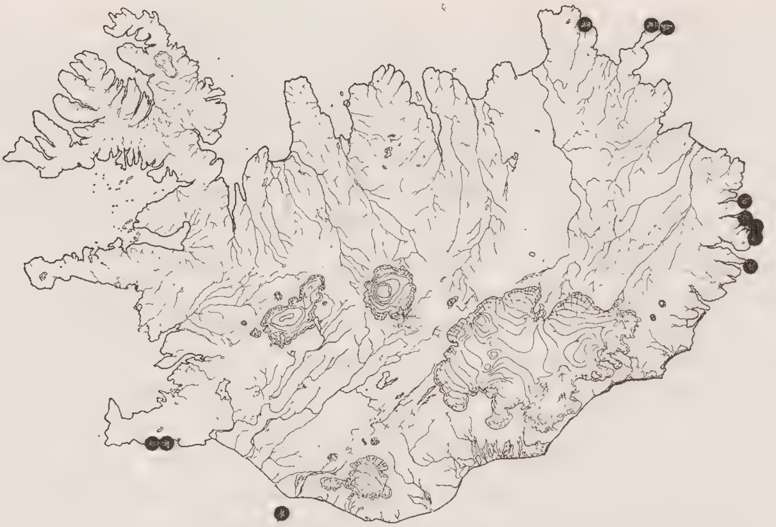


Fig. 3. The present breeding distribution of the Herring-Gull in Iceland.

Iceland between 1920 and 1930. But since then it has been increasing steadily and extending its range within Iceland correspondingly. Previous to 1920 the Herring-Gull had only once been recorded for Iceland (Húsavik 1909). Fig. 3 shows the present breeding distribution of this species in Iceland. The oldest and biggest colonies are in the central part of the east coast (Gerpir, Bardsnes). Other colonies are smaller and younger or at least discovered later. The Icelandic Herring-Gulls belong to the West-European race *Larus argentatus argentatus* Pontopp. They breed on ledges in precipitous coastal cliffs, on steep mountain slopes facing the sea, or on the top of stacks or small rocky islands.

The Lesser Black-backed Gull (*Larus fuscus* L.) has colonized Iceland simultaneously with the Herring-Gull. Previous to 1920 it had with certainty only once been recorded for Iceland (Reykjavik 1913). But after about 1920 it begins to appear annually on and off the S. coast and later on it was found breeding in several places in the south. Fig. 4 shows the present breeding distribution in Iceland of this species. In contrast to the Herring-Gull it breeds almost exclusively inland. The marginal mountains south of the big icecaps of Eyjafjallajökull and Mýrdalsjökull in the central part of the south coast constitute its main breeding area. The Lesser Black-backed Gulls of Iceland belong to the British or West-European race *Larus*

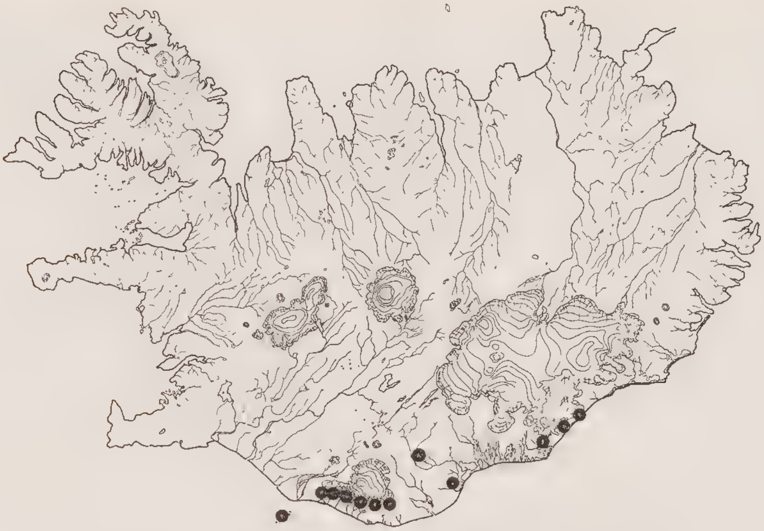


Fig. 4. The present breeding distribution of the Lesser Black-backed Gull in Iceland.

*fuscus graellsii* Brehm. Both this and the last named species have most likely immigrated to Iceland from the British Isles (or the Faroes).

The Swallow (*Hirundo rustica* L.) has for a long time been a regular and not uncommon spring visitor in South-Iceland, but in other parts of the country it is rarer. It sometimes occurs in considerable numbers, and some individuals may stay till July or August. The Swallow has been recorded as breeding in four different places in the south in this century. A pair is said to have bred on the church at Gaulverjabær (Árnessýsla) in 1911. In 1915 a pair built a nest on the gasworks in Reykjavik and laid one egg, but the pair soon disappeared. But after 1920 the Swallow has twice bred successfully in the south, one pair in the stable at the farm of Steinsmýri (Medalland) shortly before 1930, and two pairs in the stable at the deserted farm Hjörleifshöfdi (Mýrdalur) in 1930. The Swallow seems to be having difficulties in colonizing Iceland, and considering its feeding habits it is not unlikely that the main reason is scarcity of insect life. Only in the Lake Mývatn area would one think the food supply would be sufficient.

The Coot (*Fulica atra* L.) has long been known in Iceland as an autumn and winter visitor. But it was first recorded as breeding in 1891, when a nest with 7 eggs, now kept in the Reykjavik Museum, was found at Víkingavatn in Kelduhverfi (NE.). After that breeding was not recorded until 1943, when a nest with 6 eggs was found at Hvítárvellir in the Borgarfjördur (W.).

But as the nest was later deserted the eggs did not hatch. In recent years coots have repeatedly been observed during the summer and it is therefore not unlikely that it may have bred more often although no more nests have been discovered.

The Black-tailed Godwit (*Limosa limosa* (L.)) was originally confined as a breeding bird to the extensive marshy lowlands in the counties of Árnessýsla and Rangárvallasýsla in the south-west. But in 1913 it started to breed in the lowlands of the Borgarfjördur in the west. But it was not until after 1920 that it began to spread and increase to any considerable degree in this new breeding area. About the same time it was also found breeding in small numbers in several suitable localities connecting these two main breeding areas. Between 1930 and 1940 it began to appear in spring in the limited lowland districts at the head of the bays and fjords of the north coast, and since 1939 it has been breeding in the Skagafjördur and is also suspected to have bred in the Eyjafjördur.

The Oyster-catcher (*Haematopus ostralegus* L.) has always been most common as a breeding bird in the south and around the two big bays of the west coast, Faxaflói and Breidafjördur, but these areas are precisely the climatically most favourable parts of the country. In the north-west and in the western part of the north coast it has always been decidedly rarer, and in the north-east and east only single pairs used to breed locally and sporadically, while in many places it was completely absent. But in the last 20 or 30 years a considerable change has taken place in this respect, in that there has been a very conspicuous increase in the north and north-east. In the Hrútafjördur (N.) I have been able to follow this increase along a limited stretch of the coast. In the years 1910 to 1920 only 3 pairs used to breed here, but from 1940 to 1950 between 8 and 10 pairs have bred here annually.

The early history of the Gadwall (*Anas strepera* L.) in Iceland is somewhat obscure. It is first mentioned in the Icelandic ornithological literature by Faber (1822) who thought a pair of ducks which he flushed from their nest on an island in Lake Mývatn in 1819 belonged to this species. Later the Gadwall is mentioned as seen or found breeding at Lake Mývatn by Shepherd (1867) in 1862, and by a few other foreign ornithologists who visited Lake Mývatn in the latter half of the 19th century. But everyone agrees that it was very rare on the lake. Therefore there can hardly be any doubt that it has increased greatly in this century, for it is now, along with the wigeon (*Anas penelope* L.), the most common of the surface-feeding ducks of the lake. Next to them in number are the mallard (*Anas platyrhynchos* L.) and the teal (*Anas crecca* L.), and then come the pintail (*Anas*

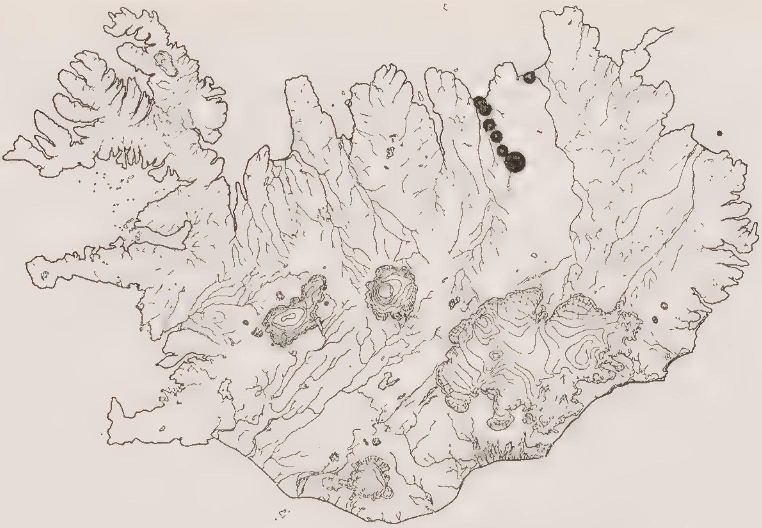


Fig. 5. The breeding distribution of the Gadwall in Iceland.

*acuta* L.) and the shoveler (*Anas clypeata* L.). As a breeding bird the gadwall is at present mainly confined to the Lake Mývatn area and the valley of the river Laxá, which is the outlet of Lake Mývatn (Fig. 5). But in recent years a few pairs have started to breed at Arnanes in Kelduhverfi some distance east of this main breeding area.

Perhaps one could find signs of changes similar to those described above among other Icelandic species of birds. Thus for instance, it might be pointed out that the gannet (*Sula bassana* (L.)), a typical Atlantic species, has after 1940 started to breed in two new localities on the north coast and in one new locality off the east coast of Iceland. It has also been maintained that the wren (*Troglodytes troglodytes* (L.)) has increased considerably in recent times, and many things indicate that this is actually so, and in any case it is not unlikely that the mild winters of recent years have created better living conditions for this species. The wren is stationary in Iceland, and the winter has undoubtedly been the critical period for this species, which in part explains the fact that it has always been rare in Iceland.

Another result of the mild winters of recent years is seen in the fact that partially migratory species now seem to winter in Iceland in greater numbers than in former times. Among such species may be mentioned the redwing *Turdus musicus* L.), the merlin (*Falco columbarius* L.), the wigeon (*Anas penelope* L.), the common snipe (*Capella gallinago* (L.)), and the redshank

(*Tringa totanus* (L.)). All these species are migratory in the north and east, but an increasing, although still small part of the Icelandic population now winters in the climatically more favourable south and south-west. And in the last few years merlins and redwings have also been found wintering in the north.

The golden plover (*Pluvialis apricaria* (L.)) is migratory in Iceland, but the exodus in autumn depends largely on the weather conditions. Owing to the mild winters of recent years it has become not unusual for great flocks of golden plovers to stay in the south and south-west till November or even December, and single birds or small flocks now occasionally winter in these parts of the country.

I shall conclude this survey of the positive changes with a fuller account of the increase in winter visitors, occasional visitors, and vagrants that has been so conspicuous in Iceland in recent years. One of the things most imperatively needed in connection with the investigation of Icelandic bird life is continuous observation all the year round in the different parts of the country. Since 1938 it has therefore been one of my principal tasks to arouse and mobilize latent interest in birds among people in as many parts of the country as possible. My efforts in this direction have proved quite successful, so that by now a small but increasing group of keen and reliable bird watchers are carrying out ringing work, making observations, and collecting birds in various parts of the country. As an example of the result of my collaboration with these people I might mention that since 1938 no less than 37 new species or subspecies have been added to the Icelandic List. Furthermore many other species which previously were known only as rare visitors or vagrants have turned out to be regular visitors. But while these results are undoubtedly partly due to the improved system of observation, I am nevertheless convinced that they are also partly the result of the recent climatic change.

A considerable part of these species belongs to the category of birds which have been called drift migrants by Salomonsen (1935), that is to say, birds of Scandinavian origin which migrate to the British Isles and Western Europe but are turned out of their normal migration route by south-easterly gales and driven towards the north-west and thus may reach Iceland. And it is only natural that such birds should now appear more frequently than before, for one feature of the climatic change is precisely a steady increase in the frequency of southerly, and especially south-easterly, winds. To these same causes we should, no doubt, also refer the big invasions in recent years of migratory butterflies, such as that of the red admiral (*Vanessa atalanta* L.) in 1947 and the painted lady (*Vanessa cardui* L.) in 1949.

Invasions of migratory butterflies on such a scale were unknown until after 1930.

Yet it is undoubtedly also due to the mild winters that drift migrants and winter visitors of southern origin have become more conspicuous in recent years. In the formerly severe winters most of these visitors very likely perished soon after their arrival in Iceland, but now they are able to maintain themselves for longer or shorter periods of time. This has even reached the point where Iceland, especially the south and south-west, has actually become a normal winter quarter for some of these species, such as the fieldfare (*Turdus pilaris* L.), the blackbird (*Turdus merula* L.), the common heron (*Ardea cinerea* L.), the common curlew (*Numenius arquata* (L.)), the lapwing (*Vanellus vanellus* (L.)), the common gull (*Larus canus* L.), and a few other species, which are now all wintering in Iceland in considerable numbers and seem to manage very well in most winters. And if the climatic improvement should continue, I am certain that some of these species will constitute the next additions to the list of Icelandic breeding birds.

The case of the curlew is particularly interesting. In Iceland we have the whimbrel (*Numenius phaeopus* L.) as a breeding bird but strictly migratory. But in winter it is replaced by curlews, probably from Norway, which winter in considerable numbers on the shores of the south-west.

## *Negative changes*

The negative changes have not been as great nor as many-sided as the positive changes I have already described, but still it can be clearly seen that some of the few arctic or high-arctic species have been decreasing in recent years. Let us take as an example the little auk (*Plotus alle* (L.)), one of the few high-arctic species breeding in Iceland. The existence of a few small colonies of this species on the island of Grímsey off the north coast has been known to ornithologists since the beginning of the 19th century. Faber (1822), who visited Grímsey in 1820, speaks of between 50 and 70 pairs breeding there, but he seems to have known of only one of the colonies. Hantzsch (1905) visited the island in 1903, and according to him the little auk was then breeding there in several places, altogether about 150 to 200 pairs. But in 1935 Holmes and Keith (1936) only found about 10 pairs breeding in the whole island, and about the same number was found by me when I visited the island in 1949. Thus since 1903 the bird seems to have been reduced from at least 150 pairs to no more than 10 pairs at the most.

Another small colony of the little auk, situated at Skoruvík, near the tip of Cape Langanes, the north-eastern corner of Iceland, was not known to ornithologists until the beginning of this century. I visited this locality in 1949 and found the colony deserted. The keeper of the Cape Langanes lighthouse told me that when he came to Skoruvík in 1882 little auks were breeding there commonly. But that since the beginning of this century they had been steadily decreasing, and that since 1928 or 1929 no birds had been seen in or near the colony. And in the last few years before that only 3 or 4 breeding pairs had been observed.

In Grímsey eggs of the little auk were for a while taken to be sold to collectors, and it has been suggested that this may have caused the dwindling of the Grímsey colony. But this explanation does not apply to the Cape Langanes colony. There no eggs have ever been taken, and the colony has never in any way been disturbed by man.

The Long-tailed duck (*Clangula hyemalis* (L.)) might be mentioned as another example of negative change. On Lake Mývatn where it formerly was the second commonest species of duck, it has decreased greatly since the beginning of this century, and has to a great extent been replaced by a new immigrant, the tufted duck (*Aythya fuligula* (L.)). The unexpected recovery in SW. Greenland of 5 long-tailed ducks ringed at Lake Mývatn may perhaps indicate that a part of the Icelandic population is retreating to that area. About the status of the long-tailed duck elsewhere in Iceland there is unfortunately no information available.

I have here attempted to outline those changes in Icelandic bird life which I believe to be first of all due to the recent amelioration of the Icelandic climate. I want to make it clear that I do not mean to assert that all the changes described here are exclusively due to these causes, but the nature and trend of these changes unmistakeably point in that direction. Thus it is significant how many of these changes have taken place after 1920 and how rapid they have been since that time, for it is precisely in the decade 1920–1930, that a very marked and sudden rise in temperature occurs in Iceland.

## References

Eythorsson, J., 1949. Temperature variations in Iceland. In "Glaciers and Climate." Geografiska Annaler 31: 36–55. Stockholm.

Faber, F., 1822. Prodr. der isländ. Ornithologie. Kopenhagen.

Hantzsch, B., 1905. Beitr. zur Kenntnis der Vogelwelt Islands. Berlin.

Holmes, P. F., and Keith, D. B., 1936. Observations on the birds of Grímsey and North Iceland. Ibis 1936: 322–330.

Müller, O., 1939. Schwarzhalstaucher auf Island. Orn. Monatsber. 47: 15–16.

Salomonsen, F., 1935. "Aves" in "Zoology of the Faroes." LXIV. Copenhagen.

Shepherd, C. W., 1867. The North-West Peninsula of Iceland. London.

# The Immigration and Breeding of the Fieldfare (Turdus pilaris L.) in Greenland

*Finn Salomonsen*

*Zoological Museum, Copenhagen*

The recent climatic change in the arctic and temperate zones of the Northern Hemisphere has caused an amelioration in the conditions of life of many animals and plants. It is a well-known fact that the breeding-area of a number of birds belonging to the Mediterranean, European or the Siberian Taiga fauna has been pushed to the north in the last decades. I have dealt with this phenomenon elsewhere (Salomonsen 1948 a, p. 85) as far as Greenland, Iceland, the Faroes and Denmark are concerned. Owing to the climatic change conditions of life in southernmost Greenland are now suitable for birds of more southern types. It was to be expected that species of the Hudsonian zone of Canada would settle in S. W. Greenland, but this has not yet happened. It is surprising, however, that a European bird, belonging to the Taiga fauna has invaded Greenland and now breeds extensively in a fairly large area of the southern part of Greenland, in this way adding an entirely new breeding-bird to the nearctic fauna. The slow occupation of adjacent areas by species increasing their breeding-area is a well-known phenomenon, but an immigration of a species in vast numbers across an enormous ocean with a subsequent successful occupation of new land is unprecedented in ornithology. Transoceanic flights of terrestrial species are known previously, but usually only a single or a few birds have taken part in these erratic movements. In one instance, however, very large numbers crossed an ocean, viz. a flock of Lapwings (*Vanellus vanellus*) of more than 1000 specimens which during a strong easterly gale crossed the Atlantic from Ireland to Newfoundland in 24 hours only (Witherby, 1929, p. 1).

The species, which has now undertaken the remarkable invasion in the nearctic region, is the Fieldfare (*Turdus pilaris* L.), an Old World species, belonging to the Taiga fauna, breeding in the northern and central parts of Scandinavia, Russia and Siberia, southwards to Germany-Hungary, and only quite exceptionally in Eastern France and in Holland. It does not breed in the British Isles, where it is a common passage-migrant and winter-visitor.

The Norwegian population of the Fieldfare mainly winters in Belgium-France and the British Isles according to the ringing results (cf. Schaanning 1949, p. 136). At the same time, however, the Fieldfare appears as a regular annual drift-visitor in the Faroes and in Iceland. Drift-visitors are birds which pass through an area in spite of the fact that the area lies far from their normal migration routes. The appearance of drift-visitors in a locality is due to the influence of adverse conditions of wind, which give the birds a drift forcing them out of their migration routes. Drift-visitors play a rôle especially on small, isolated islands as, for instance, the Faroes; cf. Salomonsen 1946, p. 45. I have dealt with this phenomenon in detail in my treatise on the ornithology of the Faroes (Salomonsen 1935, p. 218–221; map of the drift migration of the Fieldfare on p. 219) and have shown that a number of Scandinavian birds regularly occur in the autumn on the islands after easterly or southeasterly winds.

It is evident that the chances of stray southern birds occurring in the North Atlantic between Norway and Greenland increase, when the air-temperature rises during migration time. During the recent amelioration in the climate the Fieldfare has, therefore, been recorded in this area much more frequently than previously. This can be distinctly seen when going through the records from Iceland. A single specimen was obtained in the spring of 1823, on 6 Dec. 1885, on 15 Dec. 1894 and in Dec. 1900 (B. Hantzsch 1905, p. 328). In the first decade of the 20th Century it was observed 6–7 times and in the following 25 years it increased gradually. Since about 1930 it occurred annually in small flocks in the Vestman Islands (cf. Sæmundsson 1934, p. 29). The occurrence in the period 1938–43 has been described by F. Gudmundsson in a number of papers (1940, p. 21; 1942, p. 171; 1945, p. 123), and it appears that the Fieldfare is now a regular winter-visitor to most parts of Iceland. In the new handbook on Iceland birds (Timmermann 1949, p. 317) the Fieldfare is described as a regular winter-visitor occurring in flocks of 2–20 birds, occasionally in swarms of 100–200 specimens. It usually disappears some time between the end of March and the middle or the end of April. On many occasions it has been observed feeding on crowberries (*Empetrum nigrum*). The only records further north and west before the great irruption were a flock observed on Jan Mayen 4–5 May 1883, of which four were shot (Bird 1935, p. 841), a specimen (sexed as ♂) shot at the outpost Fiskenæsset, Godthåb District, W. Greenland 24 Nov. 1925 (H. Scheel 1927, p. 76) and an unsexed specimen shot at Angmagssalik, E. Greenland 1 Dec. 1935 (Hørring & Salomonsen 1941, p. 74).[1] On the N. American continent it was quite unknown.

In the middle of Jan. 1937 a large flock of Fieldfares crossed the North Atlantic. It was first traced on Jan Mayen, where several birds arrived on the 20 Jan. One bird was picked up dead and skinned (Bird 1941, p. 129). At the same time a Norwegian trapper secured a specimen (ad. ♂) near Cape Humboldt on Ymer Island in N. E. Greenland (Bird 1941, p. 129). In the last days of Jan. the irruption reached S. W. Greenland and several were observed or shot in Godthåb District on 27 Jan. A specimen shot at Kapisigdlit on this date, and another specimen shot at Qornoq on the same date (both localities are in the Godthåbsfjord) are preserved as skins in the bird-collection in the Seminary in Godthåb. Fieldfares were also observed in the Ameralik Fjord in the latter part of Jan. and the first days of Feb.; later on the birds disappeared. The Greenlanders in Godthåb, with whom I discussed the matter during my stay there in 1946, remembered very well this peculiar invasion of birds, which were completely unknown to them.

The majority of the Fieldfares hurried to the south along the west-coast, and the next day they were met with in Julianehåb District. Four specimens were shot at various localities, viz.

♂ juv. Sydprøven 28. Jan. 1937
♂ ad. Sydprøven 28. Jan. 1937
♂ juv. Lichtenau 30. Jan. 1937
♂ juv. Nanortalik 31. Jan. 1937

All four skins were sent to me by Dr. Laurent Christensen, Julianehåb; they are now in the Zool. Museum of Copenhagen (cf. Hørring and Salomonsen 1941, p. 73). No doubt many more specimens were shot there but were not skinned.

Parts of the flocks may have continued to arctic N. America. We have no certain knowledge of that, but it is of extraordinary interest that a semi-mummified skin was found in the possession of an old Eskimo woman at Jens Munk Island, at the head of Foxe Basin, by Graham Rowley during his journey there in 1939 (Taverner 1940, p. 119). It was said to have been taken during the summer of 1939, but it is not quite clear if this dating is correct; it may have been in the possession of the Eskimo woman for a longer period. Nevertheless it is the first record of this species for North America.

---

[1] Hørring and Salomonsen have erroneously given the date of capture of the latter specimen as 1 Dec. 1936. Mr. Gitz-Johansen, who presented the specimen to the Zool. Museum of Copenhagen, has informed me that it was shot one year previously.

How did this remarkable and peculiar irruption start? According to the meteorological weather-charts for Jan. 1937, it is evident that the weather over the greater part of Northern Europe and the North Atlantic was extremely unfavourable during this period, being one long succession of snowstorms. From 10. to 19. Jan. the prevailing wind in Scandinavia and the adjacent seas was S.E., but the temperature was not particularly low as the cyclonic movements carried comparatively mild Atlantic air north- and eastwards. However, constant gales and storms of the strength 8–10 (of Beaufort's scale) for a period of two or three weeks with an air-temperature of about zero naturally have a very cooling effect and to a considerable degree prevent birds from obtaining their food (berries, etc.), in this way inducing the physiological condition necessary to start a migration. The direct impulse to leave the winter-quarters and start the great flight may have been a decrease in temperature, which took place in Western Norway on 19 Jan. The temperature recorded at 2 p. m. at the coastal stations of W. Norway had for a long time oscillated between 1° and 5° C.; on 18 Jan. it was 1°–4° C., and 19 Jan. it was ÷3°–3° C. The drop in temperature was a local occurrence and was probably due to an influx of cold air from the mountains in S. Norway, where the temperature (recorded at 2 p. m.) had for some days been ÷10–÷17° C. Such a sudden drop in the air-temperature acts as a strong impulse for departure in many birds, as is known for example in the case of *Corvids* (cf. Salomonsen 1940, p. 101).

It is in my opinion quite certain that the flock must have started from S. W. Norway. Fieldfares are known to winter there commonly, though in varying numbers; in certain years they occur in enormous flocks amounting to many thousand birds (Collett 1921, p. 39). The occurrence of the Fieldfare in winter in S. Norway is very capricious; it may suddenly arrive in enormous numbers in mid-winter and again disappear after a short stay (Schaanning 1949, p. 135). This tendency to nomadism explains how the Fieldfare is capable of undertaking migrations in the middle of the winter. It is unlikely that the flock would have started from the British Isles. If leaving the northern parts of Great Britain in winter, on account of bad weather, the Fieldfares would continue the migration to the S. W. and would not come in contact with the ocean where they could be carried by the wind. Further, if they were carried away from the British Isles by the wind they could not possibly reach N. E. Greenland, when the weather conditions were such as in Jan. 1937.

When the flock of Fieldfares in S. Norway were stimulated to start the migration in the afternoon of 19 Jan. 1937 they tried to follow their normal direction of migration, to the S. W. to the British Isles. During their cross-

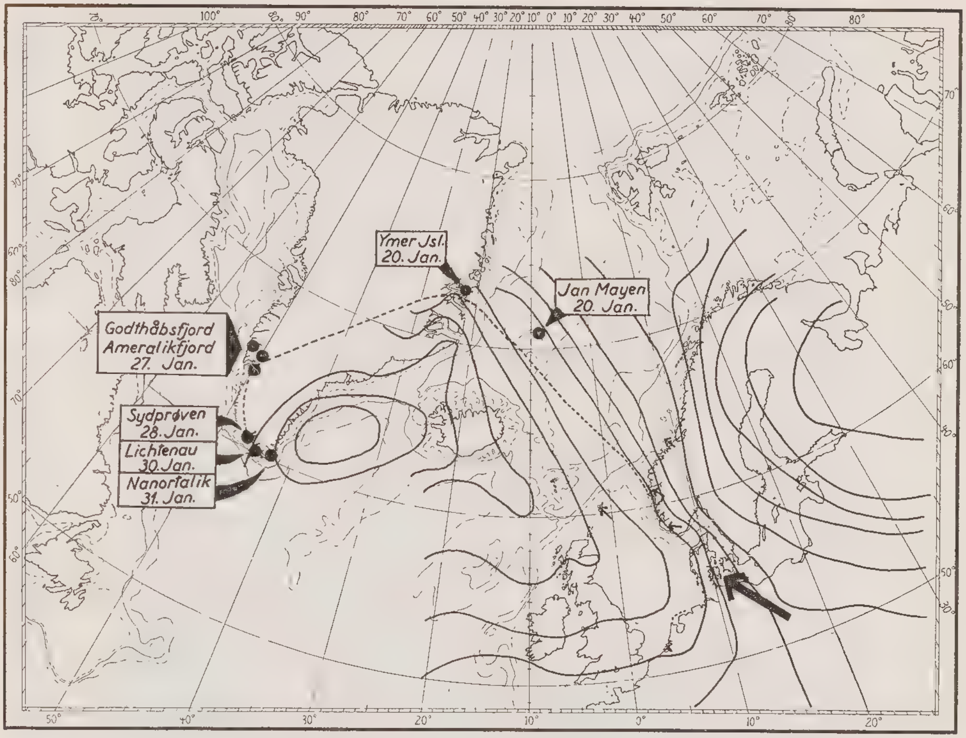


Fig. 1. The irruption of the Fieldfare in 1937. The *black circles* indicate localities where specimens have been secured, *broken line* indicates the probable course of the flight, *unbroken lines* the isobars of the 19. Jan. 1937 (at 7 p. m.) (mutual distance = 5 millibars), *arrows* direction of wind. The large arrow in Central Europe indicate the direction of wind on all stations over a large area.

ing of the northern parts of the North Sea they were carried northwards by the storm. The force of the wind was 9–10 (of Beaufort's scale) and this must have given the birds a speed of about 100 km an hour in the direction towards N. E. Greenland, the wind being S. E. (cf. Fig. 1). In the pitch-dark night they probably soon lost their orientation, and in the course of 15 to 20 hours they were carried to Jan Mayen and N. E. Greenland, arriving there on 20 Jan. In this period of the year it is dark there during 24 hours of the day. In the subsequent days the Fieldfares may have rested somewhere in N. E. Greenland, most likely in the interior of the extensive Scoresby Sound area. Then they have continued to the S. W., following their usual direction during migration, aided by the wind, which must have blown in a southwesterly direction there owing to the low pressure lying off S. E. Greenland (cf. Fig. 1). Having crossed the ice-cap the Fieldfares were observed and shot in several localities in the Godthåb District on 27 Jan. The birds continued along the coast to the south, reaching Sydprøven on 28 Jan., Lichtenau on 30 Jan. and Nanortalik on 31 Jan. The probable course of the long flight is shown as the line of dashes on fig. 1. In this figure are also shown the direction of wind (arrows) and the isobars (unbroken lines; mutual distance = 5 millibars). The above reconstruction of the irruption gives the best explanation of how it took place, and it fits in with the observations and records as well as with the meteorological conditions.

In the first years following the invasion in 1937, nothing was heard of the Fieldfare in Greenland. However, just after the world war I received some very interesting notes from Mr. Finn Christoffersen, employed at the sheep-farming control station in Julianehåb. He sent me two eggs collected by Mr. Lars Motzfeldt in July 1944 at Nunasernaq on the northern shore of Tunugdliarfik Fjord in Julianehåb District. The nest was placed in a willow-copse and contained two young besides the two eggs, which were addled. The brooding bird was described as a thrush with greyish-brown upper parts and spotted under-parts. The eggs, which measured 29.6 × 21.5 and 29.6 × 21.7 mm and were greyish-green with darker spots, clearly belonged to the Fieldfare although Mr. Christoffersen took them to be eggs of the Redwing (*Turdus musicus* L.). Mr. Christoffersen added the following remarks: "The bird and the nest were watched by Lars Motzfeldt from Qagssiarssuk and Adolf Lund from Narssak. The former was well acquainted with this bird from Qagssiarssuk (at the head of the Tunugdliarfik Fjord), where he had observed it several times and in the autumn of 1941 even saw a flock of 14 specimens. Both observers had several times met with it at Nunasernaq in summer as well as in winter. In 1943 Adolf Lund had also seen a clutch of nestlings at Nunasernaq. In 1942 a specimen was shot at Qagssiarssuk by Ole Frederiksen. In 1944 it was a common bird at Eqaluit south of the Igaliko Fjord according to Mr. Abel Kristiansen." In 1947 many thrushes were breeding at Qagssiarssuk, according to Mr. Kristen Poulsen (*in litt.* to me), and in a later letter he wrote that in 1948 at least four pairs bred at Qagssiarssuk and that thrushes were to be found in all places where there were large copses of willow. The inhabitants of Qagssiarssuk had told him that the thrushes had first appeared about 10–12 years ago.

This information clearly shows that the Fieldfare had established itself in the interior of Julianehåb District, having appeared there in about 1937, *i. e.* the summer subsequent to the invasion. In the summer of 1948

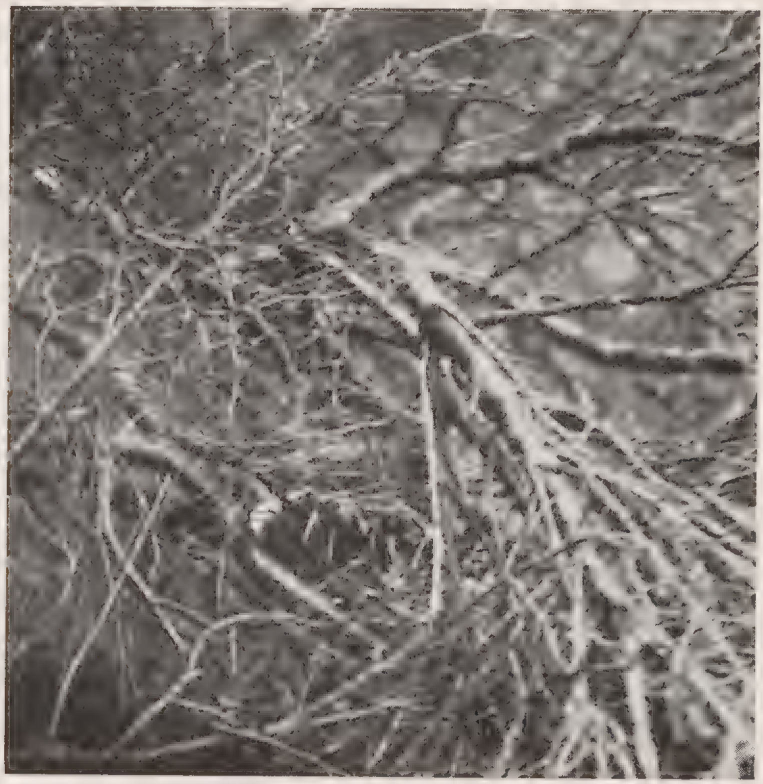


Fig. 2. Nest of Fieldfare with young, built in a birch not yet in leaf. Qanisartut 11. June 1949.

Chr. Vibe, M. sc., visited Julianehåb District and found the Fieldfare commonly breeding in the area between Igaliko Fjord and Amitsuarsuk (the northern branch of Agdluitsoq Fjord). During a subsequent visit in 1949 he collected a clutch of six eggs on 31 May at the head of Tunugdliarfik Fjord, in the vicinity of the American base Blui West One. Five of these eggs were presented to the Zool. Museum of Copenhagen; they measured: 28.8 × 20.7, 28.2 × 20.9, 27.7 × 19.9, 31.8 × 21.4 and 31.0 × 20.8 mm.

In the summer of 1949 I investigated the bird-life of Julianehåb District and was particularly anxious to study the Fieldfare, a bird with which I was well acquainted from its breeding-places in North Scandinavia. It was more numerous in Julianehåb District than I had expected, considering that only eleven years had passed since it started breeding in Greenland. At Qanisartut on the southern shore of Igaliko Fjord we found at least six pairs in the first days of June. A nest was found on 11 June with

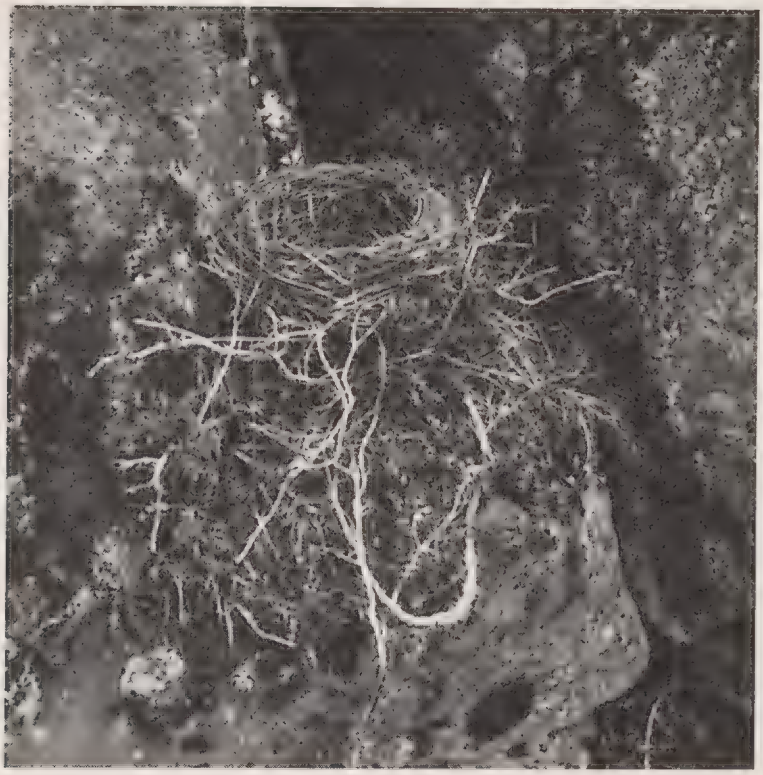


Fig. 3. Nest of Fieldfare now deserted, built on ground. Qavdlumiut 21. June 1949.

four young almost fledged. The nest was placed about one metre above the ground in a birch (*Betula tortuosa*) on a slope with S. E. exposure at an altitude of about 100 m above sea-level (Fig. 2). The birches had not yet come into leaf at this date. The nest was built of straw with a hard inner layer of mud. We saw on this date three other pairs with food for the nestlings in their bills but did not find other nests in the dense shrub of willow and birch, which was very difficult to penetrate. On 21 June Mr. Adolf Nielsen showed us a nest not far from Qavdlumiut in Agdluitsoq Fjord. Mr. Nielsen had found young in the nest earlier in spring but the nest was now deserted, and we observed two or three Fieldfares in the vicinity of the nest. The forest vegetation here was partly destroyed by sheep, and the nest was placed on the ground in a recess of the cliff on a steep mountain side (Fig. 3). It was of the same size and structure as the nest at Qanisartut. Some other specimens were observed at the head of Amitsuarsuk,

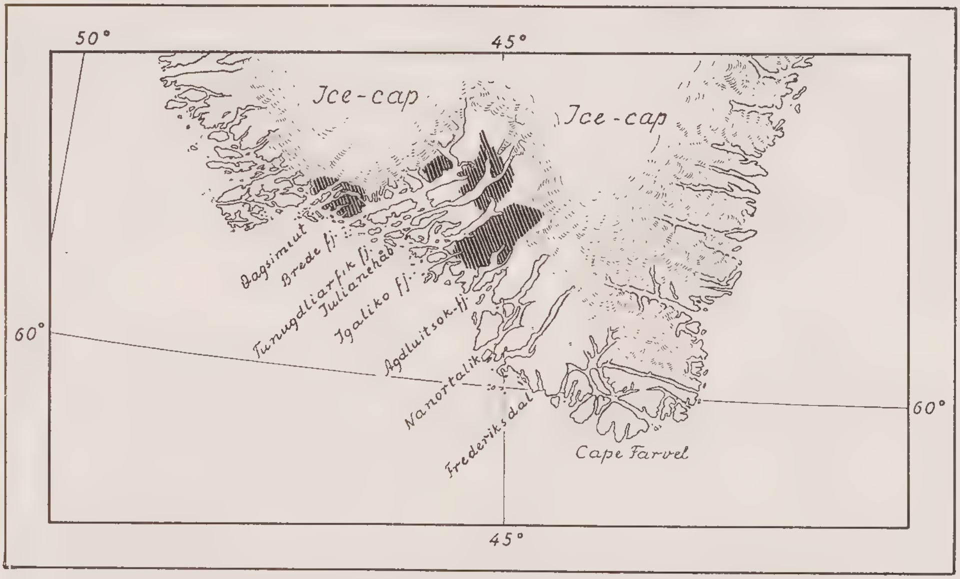


Fig. 4. Map showing breeding-area (hatched) of the Fieldfare in Julianehåb District, S. W. Greenland.

and the Fieldfare is no doubt common everywhere in the interior of the huge, densely forested country between Igaliko Fjord and Amitsuarsuk.

The life-habits of the Greenland Fieldfares do not differ from that of the Scandinavian population. I usually observed the birds on the wing as they are then very noisy, while they are difficult to find when they feed on the ground under the dense shrub. They appeared to me to be considerably shyer than in Scandinavia. The egg-laying takes place in the latter half of May, which corresponds to the conditions in S. Norway, while in N. Norway (Finmarken) egg-laying takes place in mid-June (Collett 1921, p. 95).

The Fieldfare is very familiar to the Greenlanders of the sheep-farming districts in the interior of Julianehåb District and they call it *orpingmiutarssuaq* (the big bird of the willow shrub). Its habitat is to be found in the areas covered with 1–2 m high shrub of willow mixed with forests of birch. These forested areas are only found in the interior of Julianehåb District. In the coastal regions the summer temperature is too low for the birch, and there the Fieldfare is completely absent and quite unknown to the inhabitants.

The distribution of the Fieldfare in Julianehåb District at present (1949) is shown in fig. 4. According to information received from the Greenlanders it breeds in the hinterland of Qagssimiut (observed by Klaus Poulsen), in the country north of Sermilik Fjord (Bredefjord), at Tasiussak on the southern shore of this fjord, at a number of localities at the head of Tunugdliarfik Fjord and in the interior region of the country between Igaliko Fjord and Agdluitsoq Fjord. Further south it is as yet unknown. I searched in vain for it in the fertile Qingua Valley in Tasermiut Fjord, where the largest birch-forests in Greenland are to be found. The Fieldfare was first noticed at Qagssiarssuk at the head of the Tunugdliarfik Fjord, and from here it has spread out both to the north and to the south.

It is interesting that the Fieldfare is resident in Greenland. All Greenlanders agree to this fact. Henning Lund has observed it in winter at Qanisartut, Kristen Poulsen and several others at Nunasernaq, and Adolf Nielsen at Qavdlumiut. The latter informs me that in winter the Fieldfare moves about in flocks and once he saw a swarm numbering at least 30 specimens.

The reason for the successful occupation of S. Greenland by the Fieldfare is primarily the amelioration of the climate. On the border-line of its breeding-range in Scandinavia it is very susceptible to oscillations in temperature. It breeds up to the tree-limit of the birch-zone, but in recent years it has occupied the lower part of the subalpine willow-zone in Lapland but not further south in Härjedalen, where the summer temperature has not increased to the same extent as in Lapland (cf. Salomonsen 1948 b, p. 232). The mean-temperature for July in the North Scandinavian subalpine birch-forests is about 11° C. In the inner regions of Julianehåb District the corresponding temperature was formerly 9°–10° C. but has now increased to about 11° C. In the same way the winter temperature has considerably increased, now being more than 5° C. higher than 50 years ago, thus making it possible for the Fieldfare to survive the arctic winter. Without being a resident in Greenland it would no doubt have been impossible for the Fieldfare, as a newcomer, to establish itself permanently there. If it had tried to migrate, after the first successful breeding-year so far from its normal distributional area, the entire population would no doubt have perished. A certain number have probably started migration and have succumbed in the sea. In this way selection has formed a population in which the urge for migration has been lost or at least has been considerably inhibited.

Another important fact is that the Fieldfare did not meet any serious competition in the Greenland birch-forests. This ecological niche is only inhabited by the Redpoll (*Carduelis flammea* (L.)), and in addition the Lapland Bunting (*Calcarius lapponicus* (L.)) is found in the not too forested areas. These much smaller birds were, of course, easily driven away if necessary by the aggressive and quarrelsome Fieldfare. In Iceland the birch-forests are everywhere inhabited by the large, indigenous race of the Redwing (*Turdus musicus coburni* Sh.), and this may account for the fact that the Fieldfare has not been able to establish itself in Iceland, where it is a very common winter-visitor, as mentioned above.

The immigration of the Fieldfare to Greenland is a most interesting biological phenomenon, showing an example of how a species is able to extend its distribution across an ocean to another continent when the natural conditions are favourable. The future spread in Greenland will be followed with the utmost attention.

*Discussion:*

J. S. Huxley: Could Dr. Salomonsen tell us why in his opinion the Redwing has not colonized Greenland as well as Iceland? Is it merely a matter of accident?

F. Salomonsen: I think it is a matter of accident. If the Iceland Redwing had undertaken an irruption on a large scale like the Fieldfare it would no doubt have been able to colonize S.W. Greenland. It has been captured in Greenland a number of times (both the Iceland and the Scandinavian subspecies), but always single birds only, never flocks as in the case of the Fieldfare.

G. Rudebeck: In July 1938, Mr. Gunnar Nordquist and I found the Fieldfare (*Turdus pilaris*) nesting in the alpine zone near Ammarnäs in Swedish Lapland. The nest was situated on the ground on an islet in a lake at a height of about 1100 metres, thus far above the birch- and even the willow-zone.

F. Salomonsen: The vegetation zones do not follow the climatic change until after some time and, therefore, birds may breed in the alpine zone although they belong to more southern species. This is the case with the Fieldfare which, according to older records, did not breed in the alpine zone but has now immigrated into that zone owing to the climatic change.

## References

BIRD, C. G. and E. G. BIRD, 1935. The Birds of Jan Mayen Island.—The Ibis, 13. Ser., 5.

—— 1941: The Birds of Northeast Greenland.—The Ibis, 14. Ser., 5.

COLLETT, R. 1921. Norges Fugle; in cooperation with ØRJAN OLSEN.—Kristiania.

GUDMUNDSSON, F. 1940. Fuglanýjungar I.—Náttúrufrædingurinn 10.

—— 1942. Fuglanýjungar II.—Náttúrufrædingurinn 12.

—— 1945. Fuglanýjungar III.—Náttúrufrædingurinn 14.

HANTZSCH, B. 1905. Beitrag zur Kenntnis der Vogelwelt Islands.—Berlin.

Hørring, R. and F. Salomonsen 1941. Further Records of Rare or New Greenland Birds. (Miscellaneous Notes on Greenland Ornithology IV).—Meddelelser om Grønland 131, no. 5.

Salomonsen, F. 1935. Aves, in: Zoology of the Faroes 3, part 2.—Copenhagen.

—— 1940. Kragefugle paa Christiansø.—Dansk Ornith. Forenings Tidsskr. 34.

—— 1941. See Hørring, R.

—— 1946. Den avifaunistiske Analyse og dens Terminologi. (Summary in English: The Avifaunistic Analysis and its Terminology.)—Dansk Ornith. Forenings Tidsskr. 40.

—— 1948a. The Distribution of Birds and the Recent Climatic Change in the North Atlantic Area.—Dansk Ornith. Forenings Tidsskr. 42.

—— 1948b. Fuglelivet i Härjedalen, zoogeografisk belyst. (Summary in English: The Ornithology of Härjedalen, from a Zoogeographical Point of View.)—Dansk Ornith. Forenings Tidsskr. 42.

Schaanning, H. Th. L. 1949. Bjerktrostens (*Turdus pilaris*) Trekk og Vinterkvarter.—Stavanger Museums Årbok 1948.

Scheel, H. 1927. Nathejre, *Nycticorax griseus*, og Sjagger, *Turdus pilaris*, nye for Grønland, med Bemærkninger om forskellige sammesteds sjældne Arter.—Dansk Ornith. Forenings Tidsskr. 21.

Sæmundsson, B. 1934. Zoologiske Meddelelser fra Island.—Vidensk. Medd. fra Dansk Naturhist. Forening 97.

Taverner, P. A. 1940. Fieldfare, an addition to the American list, and some arctic notes.—The Auk 57.

Timmermann, G. 1949. Die Vögel Islands.—Vísindafélag Íslendinga 28.

Witherby, H. 1929. A Transatlantic Passage of Lapwings.—British Birds 22.

# The Expansion of the Greenish Warbler (Phylloscopus trochiloides viridanus Blyth) in the Baltic Area, especially in Finland, towards North and Northwest, and its Causes

*Ilmari Välikangas*

*Zoological Institute, Helsinki*

(English summary of a paper in German, published in extenso in "Ornis Fennica," 28.)

The first specimen of the Greenish Warbler in Finland was shot in June 1935 by Heikki Suomalainen on the island of Mantsinsaari off the NE coast of Ladoga, and some other specimens were observed on the mainland in the same parish. Suomalainen's report caused other finds to be notified, the first in 1928 near Sortavala (P. Palmgren) and several others (a. o. breeding birds) from 1930–35 in other localities in SE Finland, most of them on the Carelian Isthmus between the Gulf of Finland and Ladoga. Suomalainen (1936) has given in a noteworthy paper a clear account of the expansion of this eastern species in Europe in the last decades without being able, however, to find any definite explanation of its causes.

Already around 1900 the species may have reached the South coast of Ladoga, the SE end and South coast of the Gulf of Finland, the Gulf of Riga and the East coast of the Baltic Sea. Then a standstill seems to have followed for 25–30 years, except in the West where the expansion apparently continued to SW reaching 20° E about 1925 and, as a rather narrow tongue, in 1930–35 along the S coast of the Baltic Sea the longitude of Rügen. Simultaneously with this last phase around 1930 the great N-NW expansion in the area of Onega—Ladoga—Gulf of Finland began, resulting in the finds mentioned and mapped by Suomalainen (1936).

When in the summer of 1935 I carried out a census of the landbird populations on the island of Suursaari/Hogland (Fig. 1, I) in the middle of the Gulf of Finland (Välikangas 1937), 3 singing males were observed, each in his own territory. In 1936 no specimens were found either on Suursaari or on the island of Tytärsaari (Fig. 1, II) 18 km from the former, while Putkonen (1938, Suomalainen 1936) noticed the species in 1936 in 3 places

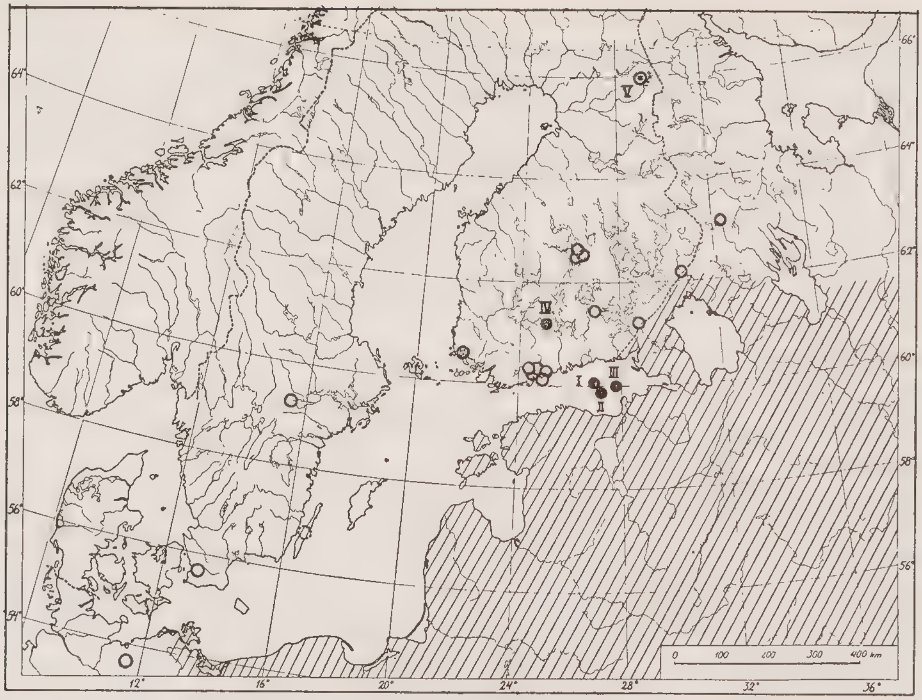


Fig. 1. The distribution of *Phylloscopus trochiloides viridanus* Blyth in the Baltic Area about 1950; breeding areas hatched, or black circles (= separate breeding localities); circle with black point = a nest find in Kuusamo, cir. 66° N; open circles = single observations.

on Lavansaari (Fig. 1, III), cir. 43 km ESE from Suursaari. In the summer of 1937 during a bird census on Tytärsaari a real invasion of the Greenish Warbler was observed from 8. VI. onwards (47 singing males in their own territories). There was also a considerable population on Suursaari in 1937. In the summer of 1938 the bird was on Tytärsaari at least as numerous as in 1937, on Suursaari probably even more numerous than in 1937. In 1939 I made a controlling tour to Suursaari and Tytärsaari as well as to the more Eastern islands of Lavansaari (Fig. 1, III) and Seiskari. On both the former islands the birds were still numerous, the species was also observed in Lavansaari.

In view of the foregoing statements it is evident that a considerable invasion of the Greenish Warbler has taken place across the Gulf of Finland towards the North. Outposts were observed on Suursaari in 1935 and Lavansaari in 1936, the real invasion occurred in the summer of 1937, probably as a continuation of spring migration from SE and guided by the islands of Tytärsaari and Suursaari in S-N direction. The first consequence was, at least, the rather numerous and continual colonization in the summers of 1937, 1938 and 1939. The later fate of these populations is unknown (the wars and the ceding of the islands in question to USSR).

On the map, Fig. 1, supplementing the map by Suomalainen (1936), is shown the distribution of the Greenish Warbler known to me in 1950. There has been a new expansion after 1935 in the areas Onega–Ladoga and Ladoga–Gulf of Finland, many new finds in South and Middle Finland, also in Esthonia, e.g. on the great islands of Ösel and Dagö (Lepiksaar 1937), and Latvia (Pētersons 1939), in the westernmost part of the South coast of the Baltic Sea, as well as in Sweden.

What has then caused the earlier expansion of the Greenish Warbler towards N and NW until 1900, the following standstill of 25–30 years, and finally the new expansion phase beginning about 1930, to which the Tytärsaari–Suursaari invasion also belongs? The species is doubtless reckoned among the typical "summer birds," appearing in their northernmost breeding areas only late in May or in the beginning of June, a group of birds whose special nature as regards recent changes of climate and dependence upon the climatic conditions in general has already been explained by Kalela (1938) and received special attention in the last years (Leivo 1946a, b; Durango 1946; Kalela 1946, 1949). It has also been proved that an actual rise in the temperature during the spring migration and the breeding season has been the most important or at any rate a very important primary cause of the expansion of many birds northwards, especially if the May and June temperatures have shown a conspicious height in the same year (Leivo 1946 b, comp. also Melander 1947, Wingstrand 1949). The May temperature would then have its great significance as the cause of a prolongation of the spring migration, the high June temperature furthering the breeding and thus a continuous colonisation in the North.

To ascertain whether changes of temperature could explain the abovementioned phases of expansion as well as the standstill of the Greenish Warbler, the average temperatures of the last decades in NW and Central Russia would be needed. They have not been available, but the figures for Helsinki/Helsingfors can be used with certain reservations (Fig. 2). The May-curve of the decennia of 1831–1940 shows that the main temperatures have risen considerably from the minimum in 1860–80 (in Oulu, 550 km to the North, from 1860) to a peak in 1890–1900. This could very well explain the earlier expansion up to the northernmost border around 1900. Then followed a colder period, in Helsinki lasting for 25–30 years, when, the May temperature did not, however, sink much below normal. This

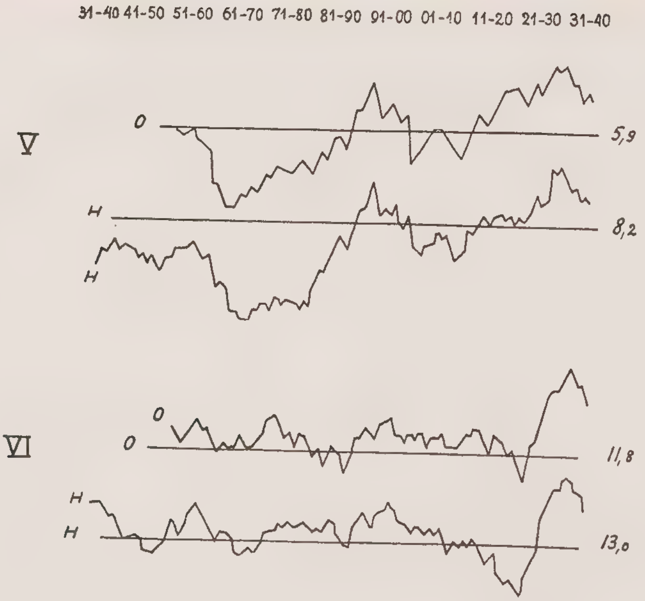


Fig. 2. The average temperatures in May (V) and June (VI) of the decennia 1831–1940; H Helsinki/Helsingfors, O Oulu/Uleåborg (after Keränen 1946).

period fits in excellently with the stagnation in the N-expansion, ascertained by Suomalainen (op.c.), and could explain it. From about 1930 a new great rise of the May temperature followed in Helsinki (from 1920 in Oulu), consequently simultaneously or a little before the last expansion phase of the species.

There is, thus, during a period of about 80 years a threefold conformity on a large scale to be observed between the expansion phases of the Greenish Warbler and the fluctuations of the main temperature in May—in my opinion a strong proof of the importance of the temperature factor for the distribution of the species.

The charts for June show smaller fluctuations, except during the period 1930–40 when the temperature reached a unique height (in Helsinki as well as in Oulu), which very likely has contributed to the survival and growth of the northern settlements near the distribution borders.

## References

Durango, S., 1946. Blåkråkan (*Coracias g. garrulus* L.) i Sverige. Vår Fågelvärld 5 nr 4: 145–190.

Kalela, O., 1938. Über die regionale Verbreitung der Brutvogelfauna im Flussgebiet des Kokemäenjoki. Ann. Zool. Soc. »Vanamo» 5 n:o 9: 1–291.

Kalela, O., 1946. Zur Charakteristik der neuzeitlichen Veränderungen in der Vogelfauna Mittel- und Nordeuropas. Ornis fenn. 23 n:o 4: 77–98.

—— 1949. Changes in Geographic Ranges in the Avifauna of Northern and Central Europe in Relation to Recent Changes in Climate. Bird Banding 22 N:o 2: 77–103.

Keränen, J., 1946. Lämpötilan muutoksista Suomessa viimeisten sadan vuoden aikana. Metsätaloudellinen Aikakauslehti 1946 n:o 11: 195–199.

Leivo, O., 1946 a. Luhtakerttu, uusin Acrocephaluslajimme. Suomen Luonto 5: 45-57.

—— 1946 b. Neue Funde des Sumpfrohrsängers, *Acrocephalus palustris* (Bechst.), in Finnland nebst einigen Bemerkungen zu seiner Ausbreitung in jüngster Zeit. Ornis fenn. 23 n:o 3: 65–77.

Lepiksaar, J., 1937. Suomalainen, H. 1936. Der grüne Laubsänger, *Phylloscopus nitidus viridanus* Blyth in Finnland etc. Eesti Loodus 5.

Melander, Y., 1947. *Locustella luscinoides* (Sav.) för första gången sedd i Norden och något om släktet Locustellas invandring till vårt land. Fauna och Flora 42 nr 6: 229–239.

Pētersons, J., 1939. Zalais kaukītis — *Phylloscopus nitidus viridanus* Blyth — Latvijā. Daba un Zinātne 1939.

Putkonen, T. A., 1938. *Muscicapa p. parva* (Pall.) ja *Phylloscopus trochiloides viridanus* (Blyth) Kaukolassa. Ornis fenn. 15 n:o 1: 48.

Suomalainen, Heikki, 1936. Der Grüne Laubsänger, *Phylloscopus nitidus viridanus* Blyth, in Finnland, nebst einigen Hauptzügen seiner Ausbreitungsgeschichte. Ornis fenn. 13 n:o 3: 89-124.

Wingstrand, K. G., 1949. Kärrsångaren, *Acrocephalus palustris* (Bechst.) i Sverige. Vår Fågelvärld 8 n:o 2: 49-74.

Välikangas, I., 1937. Qualitative und quantitative Untersuchungen über die Vogelfauna der isolierten Insel Suursaari (Hogland) im Finnischen Meerbusen. I, Die Landvogelfauna. Ann. Acad. Scient. Fenn. A. 45: 5.

# The Herring Gull - Cormorant Control Project

*Alfred O. Gross*

*Bowdoin College, Brunswick, Maine*

Along the New England coast of North America certain sea birds such as the Herring Gull *Larus argentatus smithsonianus* Coues and the Double-crested Cormorant *Phalacrocorax auritus auritus* Lesson have increased to such great numbers that the U. S. Fish and Wildlife Service, in response to numerous complaints, have adopted measures of control. If I have been correctly informed a similar problem exists on the European coast.

First I will present a brief account of the sea bird life in general and the recent changes in populations in particular which have brought about the necessity of this control. The New England coast, expecially that of the state of Maine has numerous finger-like projections that extend well out to sea. The sea between these points of land and the many bays, coves and harbors are virtually dotted with islands. There are more than 2 000 islands along the coast of Maine of varying size that support a substantial growth of trees and their countless numbers of smaller barren islands and rocky ledges. Great numbers of sea birds have taken advantage of the excellent nesting sites and isolation provided by these islands especially those lying well out to sea. Here we have the American Eider *Somateria mollissima dresseri* Sharpe, Leach's Petrel *Oceanodroma leucorrhoa leucorrhoa* Vieillot, Black Guillemot *Cepphus grylle grylle* (Linn.) as well as terns, gulls and cormorants nesting in countless numbers. We also have northern species such as the Atlantic Puffin *Fratercula arctica arctica* (Linn.) and Razor-billed Auk *Alca torda* Linnaeus meeting southern forms such as the Laughing Gull *Larus atricilla* Linnaeus to nest on the Maine coast.

The population of these birds on the New England coast is by no means static but is ever changing due to the direct and indirect competition on the part of man and in competition with the birds themselves. Certain other obscure factors causing fluctuations may also be involved.

Since the beginning of the present century the changes in populations have been spectacular. Let us take the terns and gulls as examples. There are three species of terns: the Common Tern *Sterna hirunda hirunda* Linnaeus, the most abundant, the Arctic Tern *Sterna paradisaea* Brunnich which has invaded our coast from the north and the Roseate Tern *Sterna dougallii dougallii* Montagu which is more southern in its distribution. In the past these three terns taken as a group occupied many of our islands but along with the Herring Gulls suffered greatly toward the end of the nineteenth century; due in part to the demands of the feather trade and to excessive killing and egging by natives. About 1900 favorable legislation was passed for their protection. The birds were quick to respond to this assistance and soon there were again thriving colonies of terns along the entire coast. The Herring Gulls were not so abundant at that time but by 1925 these larger and more aggressive birds began to increase by leaps and bounds. The former colonies not only contained more individuals but the gulls invaded other islands where they had never nested before. These acquired islands included many of those occupied by the smaller terns. Year after year and at island after island the terns were forced to leave until nothing but Herring Gulls were present, where a few years before thriving colonies of terns existed. By 1935 there were comparatively few tern colonies and a greatly depleted tern population. In 1928 the Great Black-backed Gull *Larus marinus* Linnaeus nested on the Maine coast for the first time and since then this larger gull from the north, like the Herring Gull has increased in numbers. By 1945 the Great Black-backed Gulls were nesting on over 100 islands and had also extended their nesting range to southern New England and even as far west as Cartwright Island, New York state. The islands selected by the Great Black-backed Gulls were in the majority of cases also occupied by the Herring Gulls. Some of these islands now have 200 to 300 pairs of Black-backed Gulls and are actually displacing the Herring Gulls.

The striking succession of birds is well illustrated by the case of Muskeget Island lying off the coast of Massachusetts where we have records going back for over 100 years. During the nineteenth century, Muskeget Island contained the largest tern colony on the American coast and no other sea birds nested there in numbers. In the latter part of the nineteenth century the Laughing Gulls invaded the island and in the course of about twenty years became well established and increased to a reported number of 20 000 birds. The terns at that time though diminished in numbers continued to maintain a foothold. In 1910 the Herring Gulls were seen there during the summer months and by 1925 these gulls were well established as a nesting species on Muskeget Island. This invasion was observed with great interest but ten years later it was regretted, for the Herring Gulls increased much more rapidly than the terns and the Laughing Gulls, much to the serious detriment of the latter. By 1947 the Herring Gulls had increased to a population of 16 000 whereas the Laughing Gulls were down to only 6 000 birds and the tern colony was represented by less than a thousand individuals. When I visited Muskeget Island last June 1949 the Herring Gulls had increased to more than 18 000 and not a single tern was nesting at the once prosperous tern metropolis. The Laughing Gulls were nesting in only a few isolated island-like groups which were completely surrounded by nesting Herring Gulls. Herring Gull nests were even interspersed among the groups of Laughing Gull nests. If the Herring Gulls were allowed to continue without control the Laughing Gulls like the terns would be extirpated in a relatively short time. Furthermore the Great Black-backed Gull is becoming established on Muskeget which would follow the pattern of succession noted on other islands.

These radical changes in population are of great interest to the ornithologist but the unprecedented increase of the gulls has been a difficult problem for the U. S. Fish and Wildlife Service. Since these birds have become so numerous complaints have poured in concerning the damage that has been done which far outweighs their usefulness as scavengers. The weir fishermen along the eastern section of Maine have been most bitter about the deluge of gulls that enter their weirs to consume much of the fish and ruin what remains before the catch can be removed. They have a just complaint.

Farmers along the coast who use waste or spoiled fish as their chief fertilizer state that after the fish has been placed on their land and before it can be plowed under, the gulls come by hundreds and remove the fish.

Owners of fine boats and yachts at some of the summer resorts along the coast have complained that the gulls concentrated in the harbors mess up their craft, wharfs and buildings.

When such an overpopulation of gulls occurs there is bound to be such keen competition for food to maintain themselves and dependant young that the birds sometimes acquire abnormal feeding habits. Along the eastern coast of Maine there is a very important blueberry industry. Surprising as it may seem the fish-eating gulls visit the blueberry plains to devour the ripened fruit. Some of the blueberry farmers have reported that whole crops were ruined by the gulls.

As a result there have been urgent demands especially from the fishing industry that the Herring Gull be taken off the protected list and that the birds be killed at every opportunity by all who wished to do so. This could not be wisely granted. To allow a mob of irresponsible persons to visit the nesting colonies to shoot the birds would undo long years of conservation and educational work directed to discouraging the indiscriminate killing of birds. It would also prove disastrous to the Eiders, Black Ducks and the many other birds which nest on the same islands and which are highly desirable to protect. For similar reasons egging could not be permitted. It was obvious that if any control was to be made it should be under the supervision of State and Federal authorities.

The U. S. Fish and Wildlife Service considered and tried various methods of reducing the numbers but finally decided on a kind of birth control, that is by destroying the eggs. For the first 5 years the eggs were needled. But this method did not prove to be very successful. When the eggs were punctured by this method they became infected and soon burst or were rolled out of the nest by the incubating bird. The gull then proceeded to lay another set of eggs and the control measures were nullified. The average gull will always lay two sometimes three or four sets of eggs if the first eggs are removed or destroyed. To make repeated visits to all of the islands along that long coast line was not practicable because of the expense and time involved. In 1939 we experimented on methods of control at the Bowdoin Scientific Station at Kent Island, Bay of Fundy, New Brunswick, Canada. After many trials we perfected an oil emulsion spray which served to close the pores of the egg and thus kill the embryos by cutting off the needed supply of oxygen. To the mixture of oil and water we added Formalin a preservative chemical. The final product was found to be a great success. The embryos of eggs in our experimental plots were killed in over 95 % of the cases. But the best feature was that the eggs remained intact and did not burst as when they were needled. Eggs so treated were incubated by the adult gull long after the eggs would hatch: to a time when the females were no longer reproductively active and able to lay another set. It is an effective and at the same time a humane method of control.

Time does not permit of presenting the details but suffice to state that since the spraying method was adopted there has been a marked decrease in the gull population. The number of gulls present in 1949 was 24 per cent less than the numbers in 1948; and 70 per cent less than the numbers that existed in 1945. You may ask: How are these percentages derived? I should explain that during the height of the nesting season there are four different divisions of operation working on different sections of the New England coast. In each division there are usually five men who do the spraying with individual spraying machines. The spraying mixture is colored with a red dye so that the eggs that are sprayed can be easily recognized from those not sprayed and thus duplication is avoided. Each man by means of mechanical counters records each egg sprayed. When an island is completed we know the number of eggs treated. Also on each island the contents of a sample of 200 or more nests are determined in order to ascertain the average number of eggs per nest on the particular island. The number of eggs is usually two or three but some have only one and a few have as many as four eggs per set. If the average for example is 2.5 eggs per nest, then the total number of eggs divided by 2.5 gives us the approximate number of nests. Each nest having a male and female the number of nests multiplied by two gives us the number of gulls nesting on the island at the time of our visit.

If we take the totals of a large series of representative islands treated in 1949 and compare them with the numbers on the same islands in 1945 we have a valid comparison and an index to the trend of the population as a whole. That is why we are able to state that the Herring Gull population in 1949 was 70 per cent less than the numbers present in 1945. To accomplish this result the U. S. Fish and Wildlife Service has treated 790 314 eggs.

I wish to strongly emphasize that there is no desire on the part of the Service, and the Maine State Fisheries Department which is cooperating in the project, to exterminate the Herring Gull. The objective is to merely reduce the numbers until they are no longer a serious menace to man's interests.

In addition to the Herring and Black-backed Gulls we have another bird which has recently appeared on the New England coast, the Double-crested Cormorant. The cormorant started nesting on the Maine coast about 1925 and from that time on it has extended its range and increased to unbelievable numbers. There are now colonies of these birds along the entire Maine coast and their breeding range has been extended as far south as islands off Massachusetts and Rhode Island.

The Cormorant does not bother the farmer but it has been the subject of many complaints from the Fishing Industry. In the past few years this bird has been included in the control project.

We confidently predict that in a relatively short time the number of gulls and cormorants will be reduced by the control measures to a point where they will no longer be an economic problem.

# The Distribution of the Kirtland Warbler (Dendroica kirtlandii)

*Josselyn Van Tyne*

*Museum of Zoology, University of Michigan, Ann Arbor*

The Kirtland Warbler, a rare "Wood Warbler" (Family Parulidae) of eastern North America, was discovered 99 years ago. The type specimen was collected by Charles Pease on May 13, 1851, near Cleveland, Ohio. His father-in-law, Jared P. Kirtland, the leading naturalist of the Mississippi Valley, gave the specimen for description to his friend and mentor, Spencer F. Baird of the Smithsonian Institution (Baird, 1852).

## Breeding ground

The breeding ground of the Kirtland Warbler was discovered by the Michigan naturalist N. A. Wood in 1903. The first nests were found in Crawford and Oscoda counties, central Michigan, but additional field work finally pushed the boundaries of the known breeding range east to Lake Huron, south to Ogemaw and Clare counties, west to Wexford and Kalkaska counties, and north to the edge of Presque Isle County. The breeding range now measures about 100 miles (160 km) by 60 miles (96 km).

On Fig. 1 a heavy line has been drawn around all known breeding records of 1903 to 1949, and within this area is plotted the major distribution of cover types. The Kirtland Warbler is found nesting only in the area of well-drained sandy soils which support pine forests (shown on the map by dots). It uses, in fact, only a small fraction of that area, nesting (on the ground) exclusively in rather dense stands of young jack pine (*Pinus banksiana*) that appear following the forest fires which so often sweep these pine plains and which actually favor the jack pine as a cover type. W. D. Sterrett (1920: 5) writes that "land composed of poor, medium-to-coarse sands or land which is impoverished by fire and on which Norway or white pine does not readily spring up and thrive is the kind on which pure or nearly pure stands of jack pine constitute one of the principal forest types

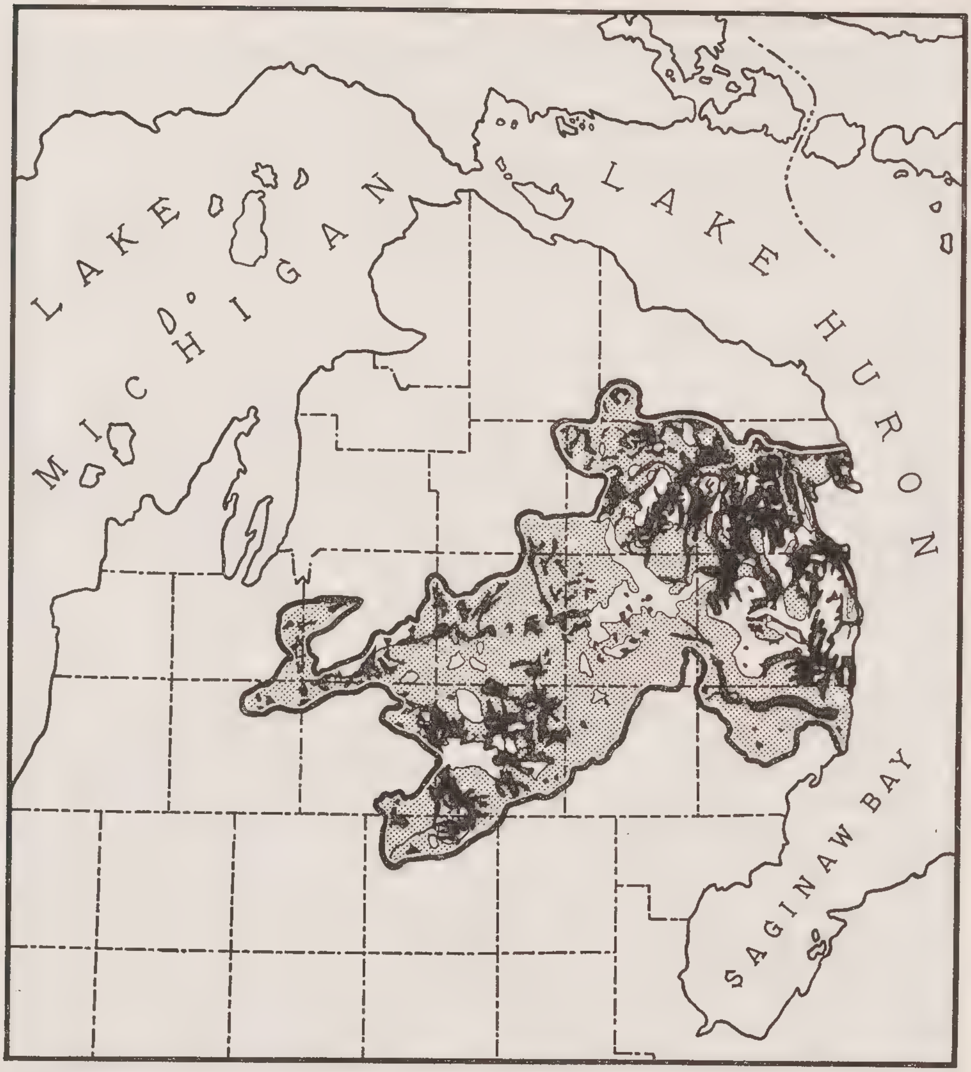


Fig. 1. Breeding range of the Kirtland Warbler. All of the known breeding records, 1903 to 1949, are inclosed within the heavy black line; within that area is plotted the major distribution of the three cover types: pine forest (dotted), hardwood forest (white), swampland (black). Cover distribution based on A. D. Perejda's map, "Original Forests of Michigan" (Wayne University Press, 1946).

of the North. Even on this land, if for a number of years fires are excluded, soil and humus conditions improve and jack pine gradually gives way to the longer-lived and more persistent Norway pine, or in some cases to spruce."

We know nothing about the aboriginal conditions under which the Kirtland Warbler bred, but there were always fires caused by lightning, and tornadoes must have occasionally leveled some stretches of mature pine, thus making way for areas of young jack pine similar to the present Kirtland Warbler habitat.

The range of the jack pine extends far outside Michigan (from Alberta and Saskatchewan east to New Brunswick and south into Minnesota and Wisconsin), but I and many others have searched in vain for the Kirtland through hundreds of square miles of apparently suitable habitat in these states and provinces. Harrington's report (1939) of Kirtland Warblers believed to have been seen near Pembroke, Ontario, has not been confirmed. In fact, we have no positive evidence whatever of the occurrence of the species in the breeding season outside of central Michigan in modern times to set against the ever-growing negative evidence provided by the failure of one investigator after another to find the Kirtland Warbler in the Upper Peninsula of Michigan or in other states and provinces. However, as explained below (*see* Spring migration), there is considerable reason to believe that at least in the late nineteenth century the breeding range extended considerably farther to the north and west.

### Winter range

The winter range of the Kirtland Warbler is almost as interesting and remarkable as its summer range, for this species is apparently the only North American bird which is restricted in winter to the Bahamas. (See Fig. 2.)

The location of the winter range was foreshadowed by Baird's discovery (1865: 207) of the October specimen taken at sea by Samuel Cabot in 1841, "between Abaco and Cuba," but not until C. B. Cory's report (1879) of the specimen he collected on Andros (January 9, 1879) was the actual location of the winter range known. In 1884 both C. J. Maynard (by January 10) and Cory (by February 12) found the species on New Providence, collecting 24 and 4 specimens respectively. In 1886 the naturalists of the Fish Commission steamer *Albatross* added Watlings Island and Green Cay to the known winter range of the species (Ridgway, 1891: 337, 338). The following year, A. H. Jennings (Jennings, 1888; Chapman, 1898, 1899) collected 8 specimens on New Providence during some general field work which began March 12, though Maynard (1895: 595) failed to find the bird there during November and December. J. Percy Moore collected a specimen at Port Howe, Cat Island, on November 20, 1890 (Academy of Natural Sciences of Philadelphia collection). In 1891 C. S. Winch added Eleuthera, and Maynard collected additional specimens there in 1897. Cory (1891: 295)

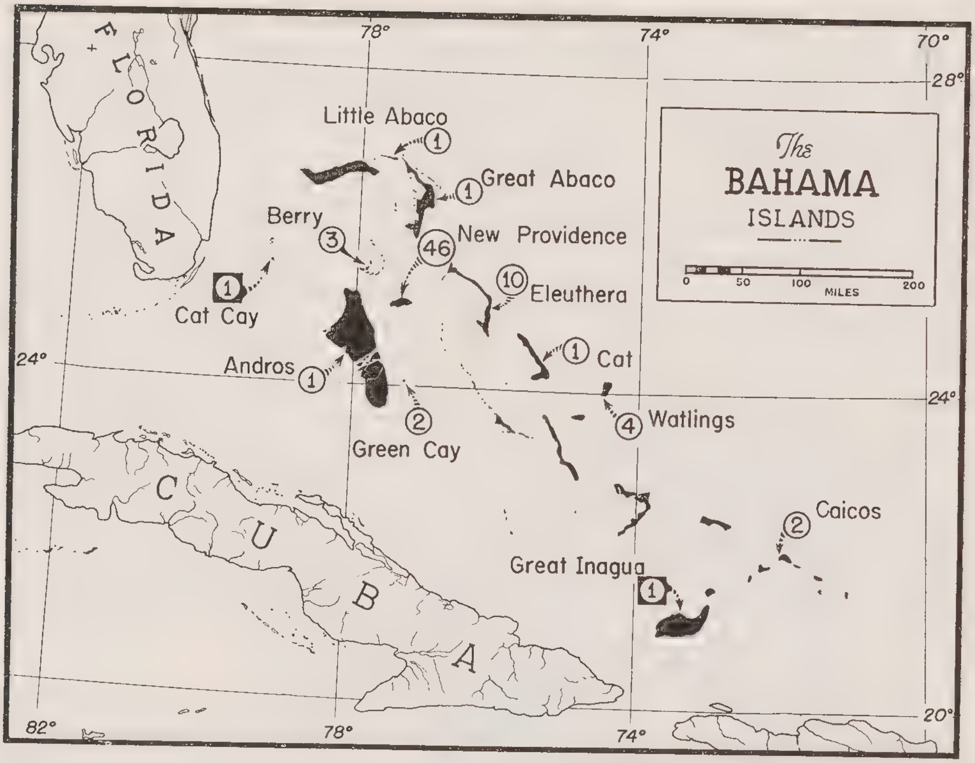


Fig. 2. Winter range of the Kirtland Warbler. All known winter records are plotted. In the circles are given the numbers of specimens known from each island; the two circles circumscribed by squares represent sight records. Arrows simply designate the islands to which the names and numbers refer—the part of an island from which the given records come is not known in most instances.

and his collector Winch found the species on the Berry Islands and on the Caicos (the latter still the southeasternmost record for the species) in 1891. Small collections made by Maynard in 1893 and 1897 on New Providence complete the nineteenth century records that I have been able to trace. In 1902 J. L. Bonhote (1903: 273, 280–281) added a record for Little Abaco and took one warbler on New Providence.

All of the records shown on Fig. 2 are represented by actual specimens except those from Cat Cay and Great Inagua. The Cat Cay record—a Kirtland seen April 28, 1907—was reported by Frank M. Chapman (1908: 224; field journal), and the Inagua record is an unpublished occurrence which James Bond has kindly permitted me to use. He saw a Kirtland Warbler there on March 8, between 1935 and 1940 (exact year not recorded).

The status of the Kirtland Warbler on its wintering ground has greatly changed since the nineteenth century, when collectors found it "fairly numerous" or "not uncommon" there. The last specimens from the Bahamas are apparently those taken by Maynard in 1913 (and possibly 1915[1]).

Others have worked extensively in the Bahamas since 1900 without finding the Kirtland Warbler. W. W. Worthington, working for Carnegie Museum, collected throughout most of the Bahamas for four months during the Kirtland Warbler wintering season in 1908 without finding the species. James Bond (letter) has studied birds on most of the major islands, spending at least 100 field days, and has seen but one Kirtland Warbler (mentioned above). In 1949 Harold Mayfield and I spent 59 man-days on New Providence and Eleuthera in January and February but failed to find the Kirtland Warbler although the study of that species was a major objective of our trip.

It should be noted, however, that during the winter season when birds cannot be found by listening for their songs, a rather large number of shy and brush-inhabiting birds, such as the Kirtland, could be distributed throughout the scattered Bahama Islands (which extend for 630 miles—1 008 km— across the ocean) without being discovered by field investigators.

## Spring migration

After spending about seven months of the year in the Bahamas, the Kirtland Warbler starts its long migration—a distance of at least 1 375 miles (2 100 km)—to Michigan. The majority of our records are spring records, but the number is still far too small, especially from the southern states, to enable us to describe the migration adequately. The conjecture has been made that the Great Abaco and Little Abaco records (March 21 and 25, respectively) represent transients and that therefore the winter range of the species does not include these northern islands, but there seems little basis for such an inference. The earliest indisputable migration record in the United States is April 12 (Cumberland Island on the coast of Georgia), and the other dates for southern states range from April 27 to May 5. To the north, in Ohio and Indiana, the dates range from May 1 to 28; in southern Michigan from May 6 to 30. According to Verne Dockham of Oscoda County, the Kirtlands arrive in the breeding area May 8 to 15.

There is not space to enumerate here the many migration records for

---

[1] The presumed 1915 specimen, now in the collection of Stephen S. Gregory, Jr., does not have the collector's original label; a copied label had been substituted before the specimen came into Mr. Gregory's possession. I have not yet been able to determine whether Maynard was in the Bahamas in 1915.

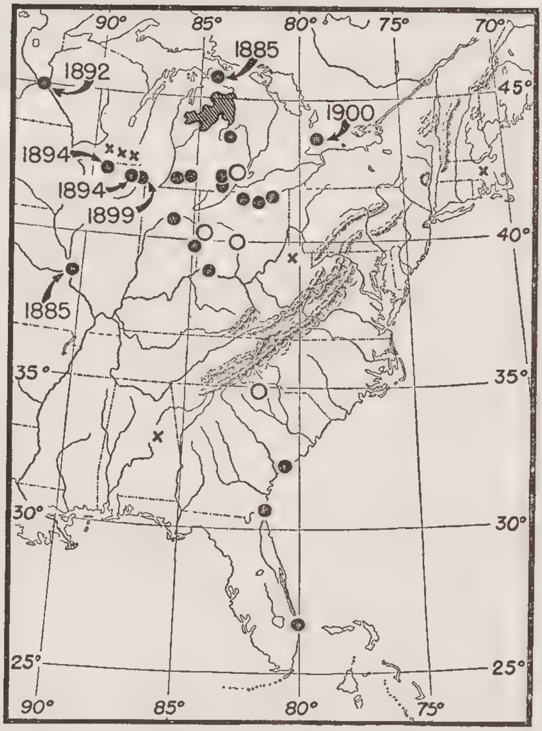


Fig. 3. Spring migration of the Kirtland Warbler. Solid black dots indicate one or more specimen records; open circles represent accepted sight records; crosses represent published reports open to doubt. The dated records, occurring from 1885 to 1900, are those of birds which seem to have been en route to some nesting ground other than that now known (Fig. 1).

Ohio, Indiana, and southern Michigan, but all of the localities are plotted on Fig. 3. Most of the spring migration records are in the direct line between the Bahamas and Michigan, but certain others (accompanied by dates on Fig. 3) are obviously far outside of any probable migration route between those two regions. It is noteworthy that these records occurred during the period (1885 to 1900) that yielded the greatest number of records on the wintering ground. The conclusion seems inescapable that the nesting ground of the Kirtland Warbler in that period was more extensive (with, consequently, a larger total population) and included areas to the north and west of the present breeding ground.

### Fall migration

As indicated in Fig. 4, there is little data available on the southward migration. Observers are, as a rule, much less active in fall, and the Kirt-

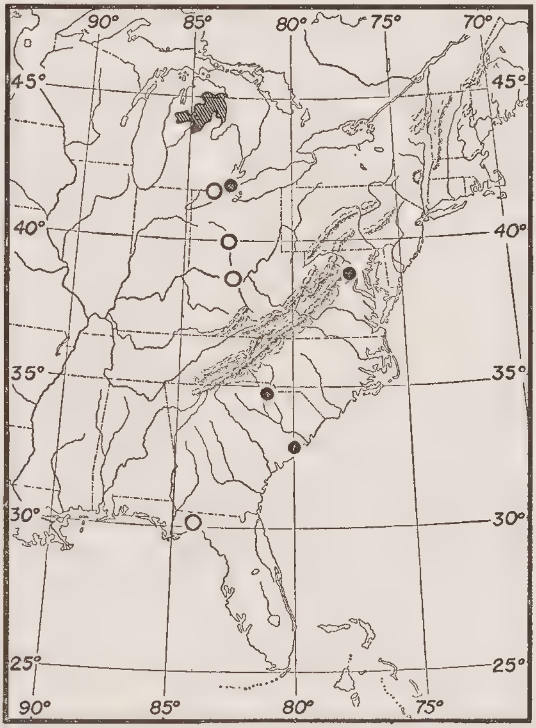


Fig. 4. Fall migration of the Kirtland Warbler. Solid black dots represent specimen records; open circles represent accepted sight records. (For his painstaking care in the preparation of this and the preceding maps, I am greatly indebted to William L. Brudon.)

land Warblers are silent then and do not attract attention. (It is surprising how many of the published spring migration records include the statement that attention was first drawn to the bird by its loud song.)

There are still no fall records for the Kirtland Warbler in Michigan south of the breeding range. Beginning at Point Pelee, Ontario, where W. E. Saunders took an immature male (Royal Ontario Museum of Zoology collection) on October 2, 1915 (an apparently unpublished record), the map shows what seems to be a rather narrow migration route along a direct line toward the Bahamas and probably crossing the southern Appalachian Mountains instead of going around their southern tip. The only other unpublished record shown in Fig. 4 is that for East Goose Creek, Florida, where Ludlow Griscom and John T. Nichols saw a Kirtland Warbler on September 9, 1919 (Griscom, letter of May 15, 1950). The northeastern Virginia record (Smith and Palmer, 1888: 148—a Kirtland collected September 25 and one seen October 2), once thought to indicate a route around the northeast end of the higher mountains, remains unique.

It is a strange fact that although the whole species must pass twice a year over the busy steamer lane between the Bahamas and the United States coast, the Cabot specimen of October 1841 (the earliest of the known specimens of the Kirtland) remains the only example ever taken at sea.

*Discussion:*

D. Amadon: Have the similar areas in adjacent states been changed in a way that would explain a restriction of the range of the Kirtland Warbler to Michigan only?

J. Van Tyne: Not as far as we know. We have studied these areas and their history, but we can offer no explanation.

R. E. Moreau asked in what circumstances the favored habitat of regenerating jack pine would have been provided in pre-human times.

J. Van Tyne: We believe that fires started by lightning and strong, local windstorms (both characteristic of that region) would always have provided considerable areas of suitable regenerating jack pine.

## References

Baird, S. F., 1852. Description of a new Species of *Sylvicola*. Annals Lyc. Nat. Hist. N. Y., 5, 1852: 217–218, pl. 6.

—— 1865. Review of American Birds. Smithsonian Misc. Collections 181, 1865: 206–207.

Bonhote, J. Lewis, 1903. On a Collection of Birds from the Northern Islands of the Bahama Group. Ibis, 1903: 273–315.

Chapman, Frank M., 1898. Kirtland's Warbler (*Dendroica kirtlandi*). Auk, 15, 1898: 289-293, pl. 4.

—— 1899. Further notes on Dendroica kirtlandi. Auk, 16, 1899: 81.

—— 1908. Camps and Cruises of an Ornithologist. N. Y.: D. Appleton & Co. 1908.

Cory, Charles B., 1879. Capture of Kirtland's Warbler (*Dendroica kirtlandi*) in the Bahama Islands. Bull. Nuttall Ornith. Club, 4, 1879: 118.

—— 1891. A List of Birds Taken and Observed in Cuba and the Bahama Islands, during March and April, 1891. Auk, 8, 1891: 292–296.

Harrington, Paul, 1939. Kirtland's Warbler in Ontario. Jack-Pine Warbler, 17, 1939: 95, 97.

Jennings, A. H., 1888. List of Birds Observed at New Providence, Bahama Islands, March—June, 1887. Johns Hopkins Univ. Circulars, vol. 7, no. 63, 1888: 39.

Maynard, C. J., [1895]. The Birds of Eastern North America. Newtonville, Mass.: Publ. by the author. Rev. edition, part 38 [1895].

Ridgway, Robert, 1891. List of Birds collected on the Bahama Islands by the Naturalists of the Fish Commission Steamer Albatross. Auk, 8, 1891: 333–339.

Smith, Hugh M., and William Palmer, 1888. Additions to the Avifauna of Washington and Vicinity. Auk, 5, 1888: 147–148.

Sterrett, William Dent, 1920. Jack pine. U. S. Dept. Agric. Bull. No. 820, 1920: 1–47, pls. 1–16.

# Food Storage, Territory and Song in the Thick-billed Nutcracker

*Per Olof Swanberg*

*Skara, Sweden*

The thick-billed nutcracker (*Nucifraga caryocatactes caryocatactes*) is found in southern and central Sweden up to the river Dalälven, 80 km north of Uppsala. A careful investigation of all known breeding localities in Sweden and Finland in the course of a study of the bird's habits has shown that the population of the nutcracker in Scandinavia, where *Pinus cembra* does not occur, must subsist on the supply of hazel-nuts (*Corylus avellana*) in the vicinity of the nesting site.

Hazel-nuts, however, are normally obtainable in nature only in a few autumn months. The nuts fall to the ground during October, and in the absence of nutcrackers they are mostly eaten or carried away by small rodents before winter. But as early as the end of August the nutcrackers begin to store up nuts, which they carry in their throat-pouch from the hazel-coppice to some place more or less deep in a coniferous wood. Their habit of carrying and storing the nuts of hazel or *Pinus cembra* has been known for a long time in different parts of Europe, and their life during two or three autumn months is actually completely devoted to food storage.

When the work begins in earnest, the nutcrackers leave their haunts in the spruce forest early in the morning, generally before sunrise, and fly direct to the hazel-coppice, which is often several and may be as much as six kilometres away. Within an hour of sunrise many have returned, loaded with nuts. These are stored in small heaps of different sizes, sometimes only three or four, often eight or nine, in the ground. The stores are laid at a depth of a bill's length, or under the lichen or moss cover of a rock. The first picture, which is from one of the islands of the Åland archipelago, shows such a store. I watched the nutcracker through my glasses and saw how and where it hid its nuts, and later I went to the spot. Although I knew exactly where the nuts lay, it was impossible to find anything on the surface which betrayed their position. But by turning the lichen cover I exposed

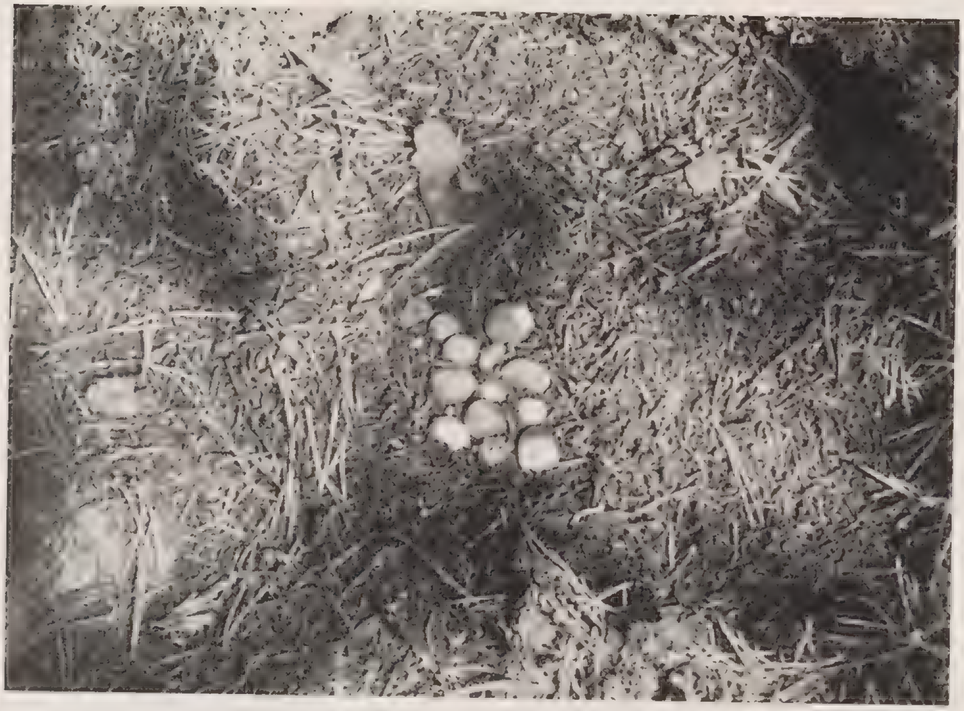


Fig. 1. A nutcracker-store consisting of 18 nuts. The lichen cover is turned over. Only the upper layer is visible.

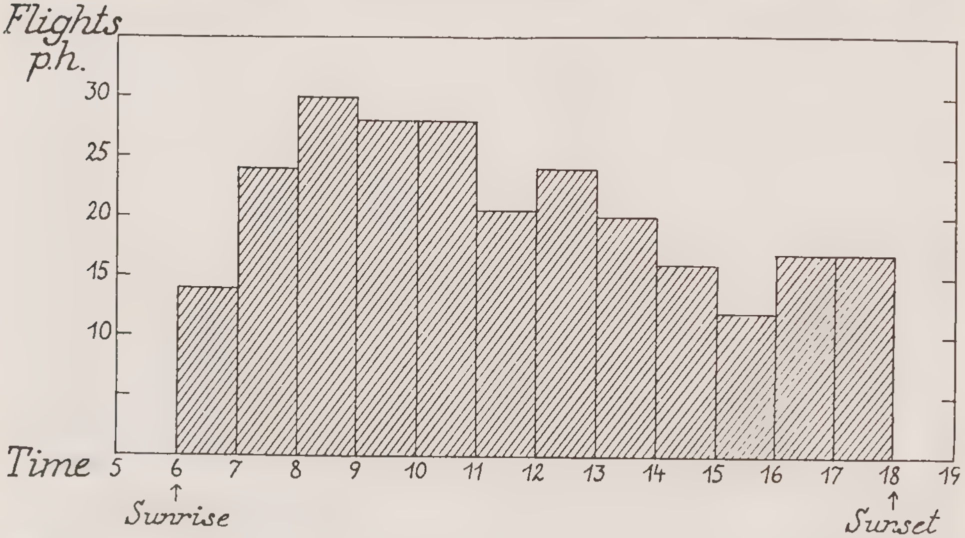


Fig. 2. *Nucifraga c. caryocatactes.* Billingen, Central Sweden. Number of flights of birds carrying nuts in throat-pouch, observed from a fixed point in territory A, September 26, 1948.

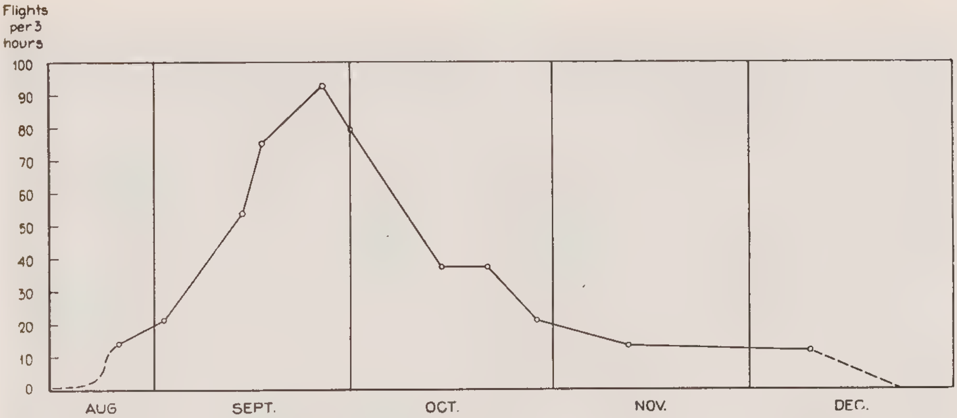


Fig. 3. *Nucifraga c. caryocatactes.* Billingen, Central Sweden. Frequency of food storing. Number of flights, with nuts in throat-pouch, observed in three-hours periods between sunrise and noon, Aug.–Dec., 1948, from a fixed point in territory A.

them to view (Fig. 1). The heap consisted of eighteen nuts, which had been neatly arranged in two layers like sardines in a tin.

When the birds are engaged in storing, they do not stay longer in the forest than is necessary for hiding the nuts. Three minutes after they arrive, on an average, they return to the hazel-coppice. The work proceeds fairly regularly throughout the day. By way of an example I have marked in a diagram (Fig. 2) the number of times nuts have been carried by several nutcrackers which I watched during one of many observation days. As you see, the birds were very busy all the day. They began to arrive with nuts seventeen minutes after sunrise and stopped only at sunset.

The nutcrackers carry nuts throughout the autumn as long as nuts are available. The frequency of their journeys was studied in different years. Diagram No. 2 (Fig. 3) is from 1948 when the crop of hazel-nuts was a rich one. It is based on observations from a fixed point and calculated from the number of journeys observed in three-hour periods. The top of the curve shows that storing activity is at a maximum when the nuts are ready to drop. It will be seen that during a great part of the year, normally about three months, the nutcracker works for its future subsistence from morning to evening with an intensity which can be compared with that of man.

Such a pronounced habit of intensive and specialised work could hardly have developed if the nutcracker had not succeeded in making use of its stores. Carl von Linné (1748–52: 94), in his lectures here in Uppsala two hundred years ago, said that the nutcracker "as the farmer says takes the clouds as a mark" when it hides its nuts, and so will not be able to find them again.

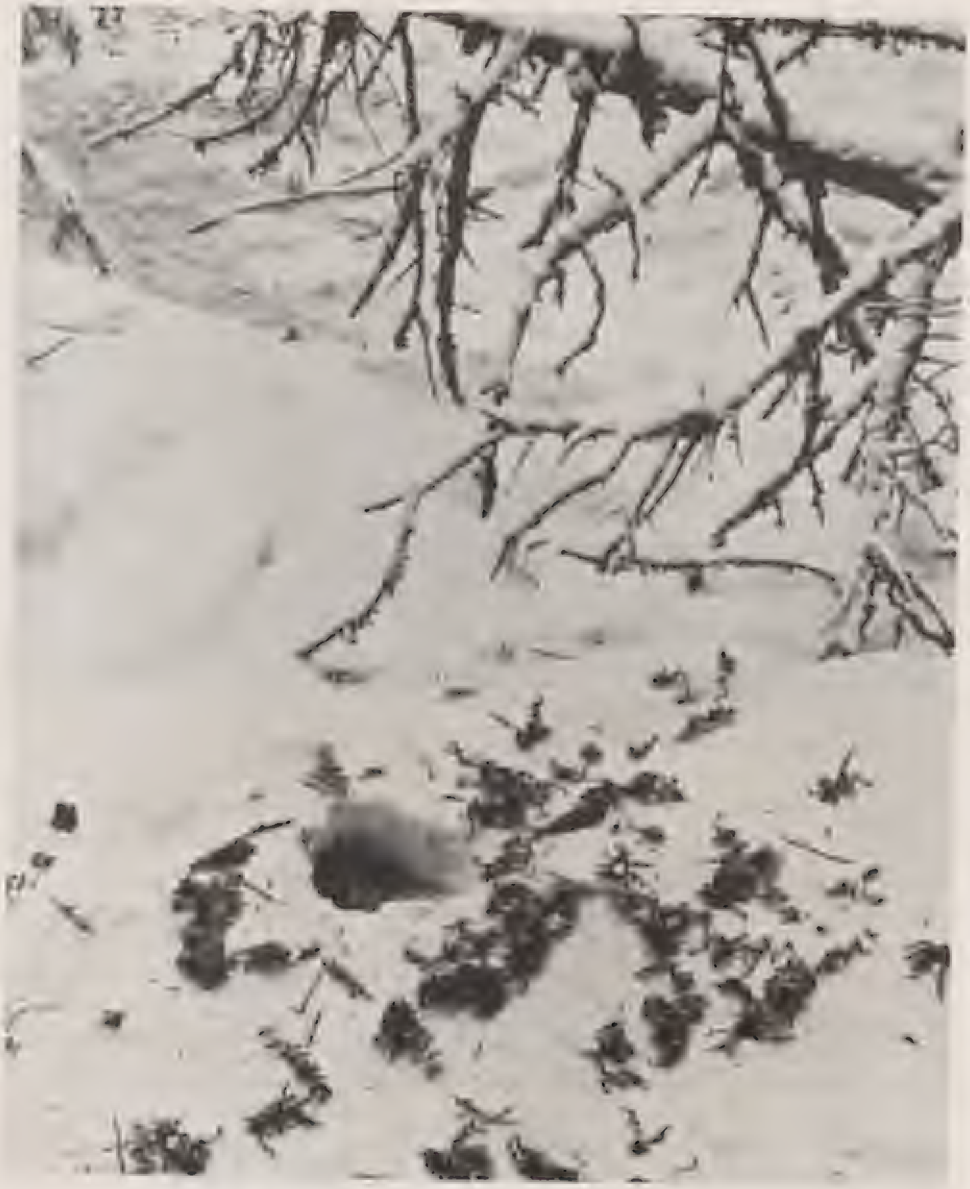


Fig. 4. Excavation in the snow where the nutcracker has dug out its nuts.

Many more recent writers have made similar assumptions. Yet ornithologists have recorded some instances of a nutcracker finding its stores again (Studer & Fatio, 1901: 314, and others).

In point of fact in the spring the nutcracker still has such a large supply of hazel-nuts that the principal part of the food of the young in the nest consists of nut kernels. For it has a fantastic power of rediscovering its stores. Every day in winter it digs out nuts from one or more hiding places. The stores may be snow-covered, sometimes for several months, but this does not deter the birds, for they can find their stores even under eighteen inches of snow.

One photograph shows a typical example of a store that has been dug out by a nutcracker (Fig. 4). Heinroth's (1924–28: 259) experiments with the raven (*Corvus corax*) and my own with the nutcracker have shown that the bird cannot conceivably have been aided by the sense of smell. On winter days which offered optimum conditions of observation I have counted the number of excavations in the snow with nutshells in or near them, and also the number of excavations where there were no signs of the bird having found its nuts. Out of 351 such excavations which I have examined, the nutcracker had succeeded in finding its nuts in 86 per cent. This figure is in fact considered to be too low as an index of the retentive power of the nutcracker's memory.

It is of special interest that almost one-third of these records occurred in each of the months, January, February and March (in the March group I have included the few April records), and that the percentage of successful excavations in snow is practically the same for all three months, viz. 86 per cent. This indicate that the nutcracker has a kind of abstract recollection, which, figuratively speaking, helps it in remembering which stores were used earlier in the winter. Thus it practically never searches for a store already emptied, even if new snow has fallen. Another picture (Fig. 5) shows the small depression in the ground out of which six nuts were dug. It is evident from the appearance of the excavation that the bird did not have to seek for the nuts.

Each pair has its special area in the coniferous wood. In my experience, after ten years' study, nutcrackers hold their area, when they have found a suitable one, for life. The sketch-map (Fig. 6) shows the living area beyond the boundaries of which my best-known pairs of nutcrackers will never, or at any rate only for a short distance, move. To the right is the spruce forest on Billingen mountain, then comes the slope of the mountain covered by deciduous wood. To the left is the low-lying, partly cultivated

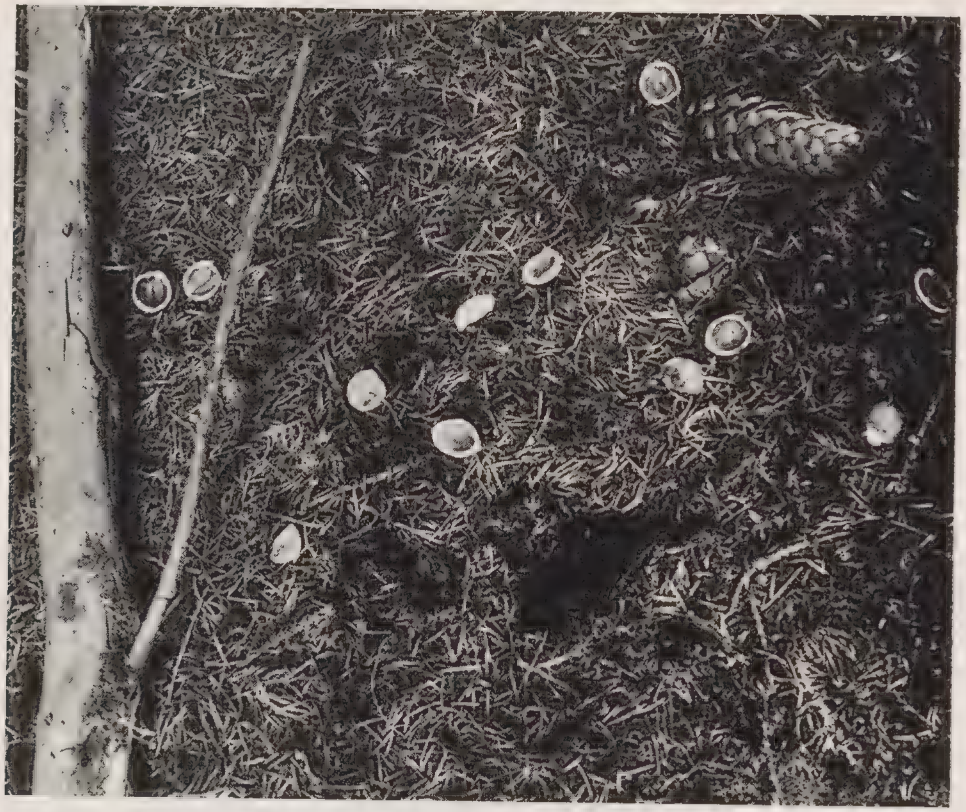


Fig. 5. The small depression in the ground out of which six nuts were dug under the snow cover shows that the nutcracker did not have to seek for the nuts.

country. Each black spot marks a group of hazels. On the right I have drawn the approximate boundaries of the areas on the plateau-top of the mountain which are occupied by the different pairs of nutcrackers. These areas average 13-14 hectares. The rest is communal feeding area.

In my notes I have always called these special areas 'territories'. But in more careful descriptions I have often used more cautious terms, on account of the well-known definitions of territory given by Mayr (1935), Noble (1939), N. Tinbergen (1936, 1939), Nice (1943) and others, which claim that a territory should be defended "by a fighting bird against individuals of the same species and sex" or the like.

In spite of intensive studies of nutcrackers for many years, I have never observed any true territorial fights or any consistent defence of the territory against intruders by means of sounds or posturing. Nevertheless, each pair

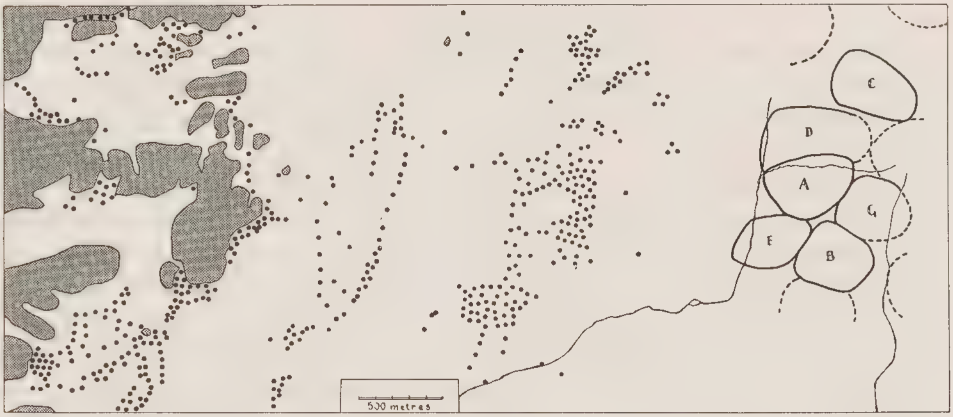


Fig. 6. Living area of some pairs of nutcrackers. Billingen, Central Sweden. To the right the territories in the spruce forest. In the middle and to the left is communal feeding area. Each black spot marks a group of hazels.

obviously has its defined territory. As an example, my nutcracker pair A are proved to have held the same territory for at least ten years. During this time I have found fourteen nests of A in it, but although A has always been surrounded by other pairs, other nutcrackers have never made any attempt to nest in the same area. Broadly speaking, the areas are used only by their holders, but it is not unusual for other nutcrackers to trespass and rest in them without being attacked, and sometimes they may even pay friendly visits to each other, as during the ceremonial gatherings, which take place early in the morning immediately before or during nest-building. During these gatherings neighbouring birds meet pair A in A's area, probably without any practical purpose and without the owners making any attempt to chase them out of their territory.

It should, however, be added that nutcrackers pair for life, and that their territory corresponds in its general type to that of such birds as the chaffinch (*Fringilla coelebs*), the reed-bunting (*Emberiza schoeniclus*), the snow-bunting (*Plectrophenax nivalis*), which Howard called "breeding territory" and N. Tinbergen "sexual territory". These sexual territories, according to Tinbergen and others, are defended "shortly before and during the formation of a sexual bond", and for several reasons the formation of the sexual bond in the nutcracker is very difficult to observe. Thus I cannot deny the possibility that the nutcracker may in fact defend its territory with actual fighting during the short time of pairing up and establishing a new area. On the other hand Mary Erickson (1938) has pointed out that in the wren-tit (*Chamaea fasciata*), which holds territory continuously throughout the year and retains the same territory for a number of years, probably for life, "fighting was observed in all months of the year". Moreover, Angus Robertson (1949: 301) has pointed out that in south-western Australia many birds defend a territory to a certain extent all the year round, and that, for instance, butcherbirds (*Cractias*) and kookaburras (*Dacelo gigas*), which "defend permanent territories in pairs . . . will foregather at times even during the breeding season, with neighbouring members of the species, . . . well within one or the other pair's territory without friction".

It is, however, a fact that every pair of nutcrackers disposes of a special area throughout the year, and that the right of possession of this area is respected by other nutcrackers without actual territorial fights. Thus this area can hardly be described by the ornithological technical term 'territory', although more than most bird-territories it corresponds to what human beings mean by territory, and in spite of the fact that its purpose corresponds to that indicated by Howard (1920) when he wrote that "securing a territory is (then) part of a process which has for its goal the successful rearing of offspring".

In defining territory some authors consider it wrong to include any reference to the function of territory, as the function may be, and in fact is, so different for different species. Thus the territorial fights or the mere symptom of establishing the territory are regarded as the prime consideration, and such definitions of territory approximate rather to definitions of the use of the technical term 'territory'. But this leaves us with no general designation for the phenomenon of such vital importance to the bird, which the breeding territory in a deeper sense represents and which is expressed by each pair securing a territory, although we may call this phenomenon "breeding territory," "sexual territory" or the like when fights occur as indications of this function.

In my opinion it is, however, justifiable also to regard as breeding territory an area like that of the nutcracker, which is the property of a single pair of birds in a considerably stricter sense than, for instance, that of a chaffinch (*Fringilla coelebs*). Although it is not defended in the true sense of the word, and intruders are not chased away, the territory is proclaimed throughout a great part of the year. It applies to the nutcracker as well as to the wren-tit (*Chamaea fasciata*) that "the general impression is not of birds continuously exerting pressure or sparring for an opening, but rather of their acceptance of the existing status" (Erickson 1938: 263).

The purpose of territory in the nutcracker seems to be to secure every pair a certain area of their own, which they get to learn in every detail and which thus ensures particularly good shelter for the adult birds, their nest and offspring, and which above all is suitable for well scattered and adequate stores for the winter, which are of vital importance at any rate for the populations of *Nucifraga caryocatactes caryocatactes* which, in Scandinavia, have to feed on hazel-nuts.

The function of proclaiming the position and boundaries of the territory, which is ascribed to the song of many territorial birds, is probably exercised by the harsh cries of the nutcracker, audible for a long distance. These cries have many functions, but one of them seems to be the proclamation of the territory. This is indicated partly by the behaviour of the birds, partly by the frequency of the cries.

The song, on the contrary, is weak and can hardly serve as advertising song. As song I do not consider the many different notes which are mainly heard during ceremonial gatherings before nesting and in late summer. In my opinion the actual song consists of the various piping, whistling and whining notes, which are uttered rhythmically, more or less regularly interspersed with distinct clicking sounds, and by the male only. During the song the bird takes up a position with its bill upwards and the throat dilated. Singing from the top of a tree, however, is rather abnormal, and the bird usually sings in a concealed position at a low height above the ground. Even this supports the view that it is not an advertising song indicating the territory for rivals or attracting a mate.

I have only heard the song during a few weeks before and during nest-building. Often the male interrupts nest-building for a short song. Of the different functions which have been ascribed to bird-song in general (Armstrong 1942, 1947: 294), the only one which seems to apply to the nutcracker is that of facilitating the synchronisation of the male and female sexual cycles. Armstrong says that another function of song is to indicate the stage the bird has reached in its sexual cycle. This of course can also apply to the song as an independent function, but in my opinion in the nutcracker it only forms part of the above-mentioned facilitating of the synchronisation. In other words, it is a mere mating song, which despite its pronounced subdued character must not be confused with sub-song. It is interesting to compare conditions in Australia, where according to Robinson (1947: 11; 1949: 293) many birds are resident territory-holders, and mating songs are therefore prevalent and of vital importance for them.

## References

Erickson, M. M., 1938. Territory, annual cycle, and numbers in a population of Wren-tits (*Chamaea fasciata*). Publ. Zoöl. Univ. Calif. Vol. 42, No. 5: 247–334.

Heinroth, O. & M., 1924–28. Die Vögel Mitteleuropas, I. Berlin.

Howard, E., 1920. Territory in bird life. London.

Linné, C. von, 1748–52. Föreläsningar över djurriket. Edited by Einar Lönnberg, Uppsala 1913.

Mayr, E., 1935. Bernard Altum and the territory theory. Proc. Linn. Soc. N. Y., 45–46: 24–37.

Nice, M. M., 1943. Studies in the life history of the Song Sparrow, II. Trans. Linn. Soc. N. Y., 6: 1–328.

Noble, G. K., 1939. The rôle of dominance in the social life of birds. Auk, 56: 263–273.

Robinson, A., 1947. Magpie-Larks—a study in behavior, Part 3. Emu, 47: 11–28.

—— 1949. The biological significance of bird song in Australia. Emu, 48: 291–315.

Studer, Th. & Fatio, V., 1901. Katalog der Schweizerischen Vögel, III Lief. Bern.

Tinbergen, N., 1936. The function of sexual fighting in birds and the problem of the origin of "territory". Bird-Banding, 7: 1–8.

—— 1939. The behavior of the Snow-Bunting in spring. Trans. Linn. Soc. N. Y., 5: 1–95.

# Data on the Excavation of the Nest Hole and Feeding of the Young of Green Woodpecker (Picus viridis)

*H. R. Tutt*

*Hadleigh, England*

## *Winter boring of nest hole*

Mr E. T. Cluff of Hadleigh, Essex, England, had a pair of Green Woodpeckers (*Picus viridis*) nesting in an ash tree in his garden for 3 years in succession. A nest hole was commenced in November 1946; this was visited sporadically till April 1947 and slight chipping was done at the hole during several of these visits; the boring went ahead normally in April and early May, a brood being successfully reared. A second hole was begun in November 1947, the birds following a procedure similar to that of 1946–7, and a brood was successfully reared in the second hole in 1948. A third hole was begun in November 1948, and again worked as described on the first hole, but just as this third hole was completed, Starlings (*Sturnus v. vulgaris*) introduced nesting materials and the woodpeckers deserted the hole. These facts seem to show that green woodpeckers pair for life and that selection of the nesting site and some work upon it was done almost six months before the nesting season.

A reference to winter boring of this species was recorded in "The Zoologist" No. 728 Feb. 1902 by the Rev. J. G. Tuck.

## *Description of nest holes boring*

In the first stage of boring the bird made a hollow inverted cone in the tree; the wood was attacked with such rapid blows that the sound was like drumming, and the head looked a blur: the chips were just dropped or flicked to one side.

The hole was then made a horizontal cylinder, the full diameter of 5.8 cms to a depth of 15 to 16 cms. For much of this work the head was right inside the hole and the body outside with the tail tight against the trunk, the two forward claws grasping just inside the hole and the two rear claws on the bark just under the lip of the hole—the use of the zygodactyle feet was well shown in that position. When the downward boring took place, the work on the forward portion was as described, but as the bird worked further and further inwards to the further side of the hole, it sat horizontally in the hole, the tail pointing downwards to the ground and then with the whole body inside, the tail only protruding. The work was obviously most difficult for the birds—the shoulders practically fitted the hole and the head room was very little. One difficulty seemed to be the lack of air. The shoulders almost plugged the hole; when the bird withdrew the feathers of the mantle and wing coverts were very ruffled. Hence work was in short periods varying from 1 to 3 minutes. The head was withdrawn and the bird grasping the lip of the hole, as described above, sat quite still resting, the tail tight against the bark, for periods of 1 to 5 minutes. Chips were then picked up rapidly, one by one, and flicked over the shoulder or to one side as the head was withdrawn each time.

As soon as room was secured the birds turned in the hole to come out, and after this the chips were put out from inside—2 or 3 in the bill at a time, the head appearing at the mouth of the hole; the beak was flicked and the chips flew out. As the downward boring proceeded the number of chips picked up in each beak full was from 6 to 10, and this was probably due to the chips collecting in a heap in the base of the downward boring.

Once the birds could turn round, fewer rest periods were taken outside, but the bill of the bird could be seen occasionally in the mouth of the hole, quite still, as though rest was taken inside, but the outside periods of rest were longer being from 2 to 6 minutes. Chiselling went on for 5 to 15 minutes before the chips were put out. Once 80 beaks full were removed in succession and took 8 minutes, this by the male; other numbers of beaks full ranged from 16 to 54. Neither bird put out chips if the other arrived to change over when boring was progressing. The fresh bird removed the chips on entering the hole.

Whether there was a change-over, or whether either bird came to a vacant hole, there was a call every time of "skee, skee, skee, skee,—." Only very occasionally did the two birds come to the tree together. Timed periods of work in minutes were:—

$$\left.\begin{array}{l} ♀\ 24,\ 30,\ 38,\ 61,\ 47,\ 47. \\ ♂\ 67,\ 62,\ 39,\ 26,\ 58,\ 48. \end{array}\right\}\text{ when no disturbance took place,}$$

Average ♀ 41 minutes, ♂ 50 mins.

except in the case of the male working for 67 minutes: a man came with a barking dog, which caused the bird to go. Mr McCormick recorded the

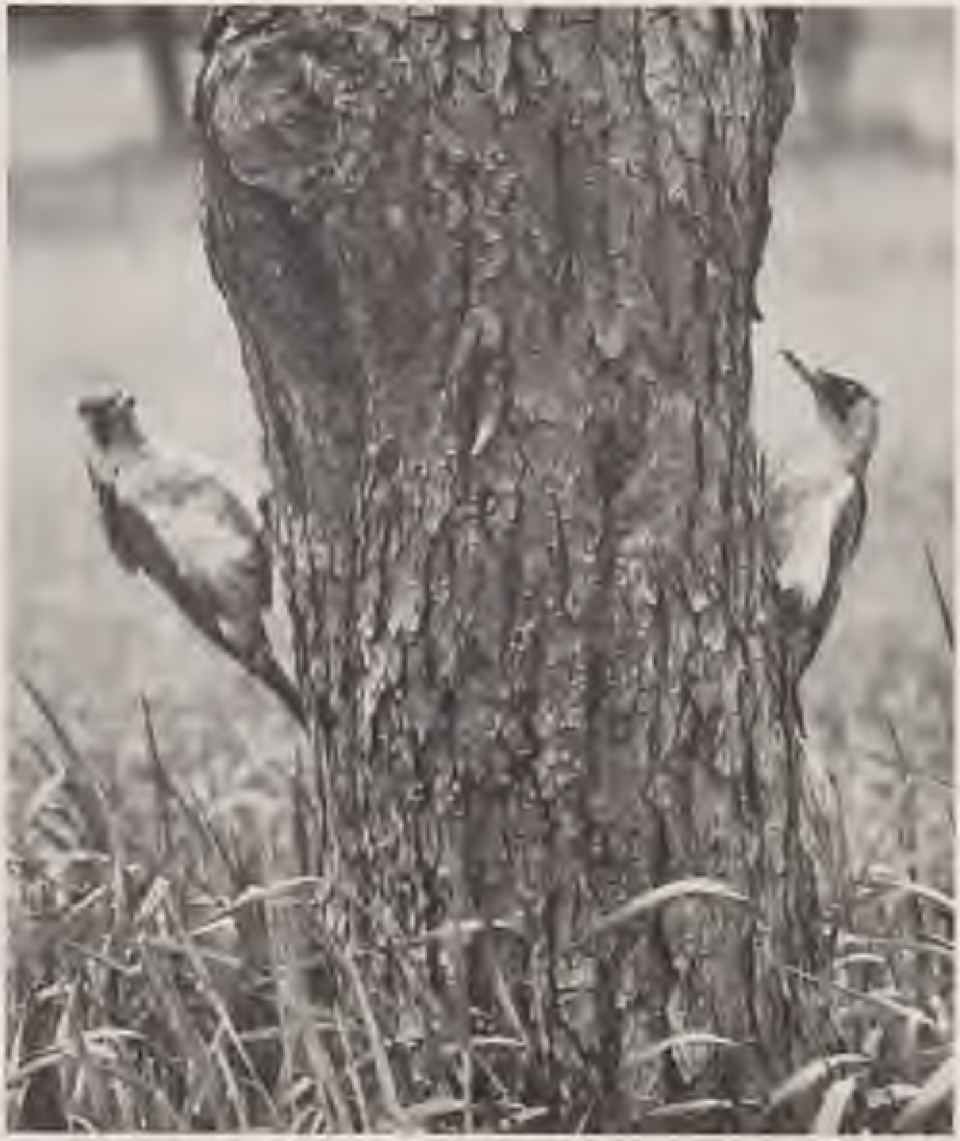


Photo by G. Lawrence.

Fig. 1. Green Woodpeckers on apple tree. Male left, near the hole. Female right.

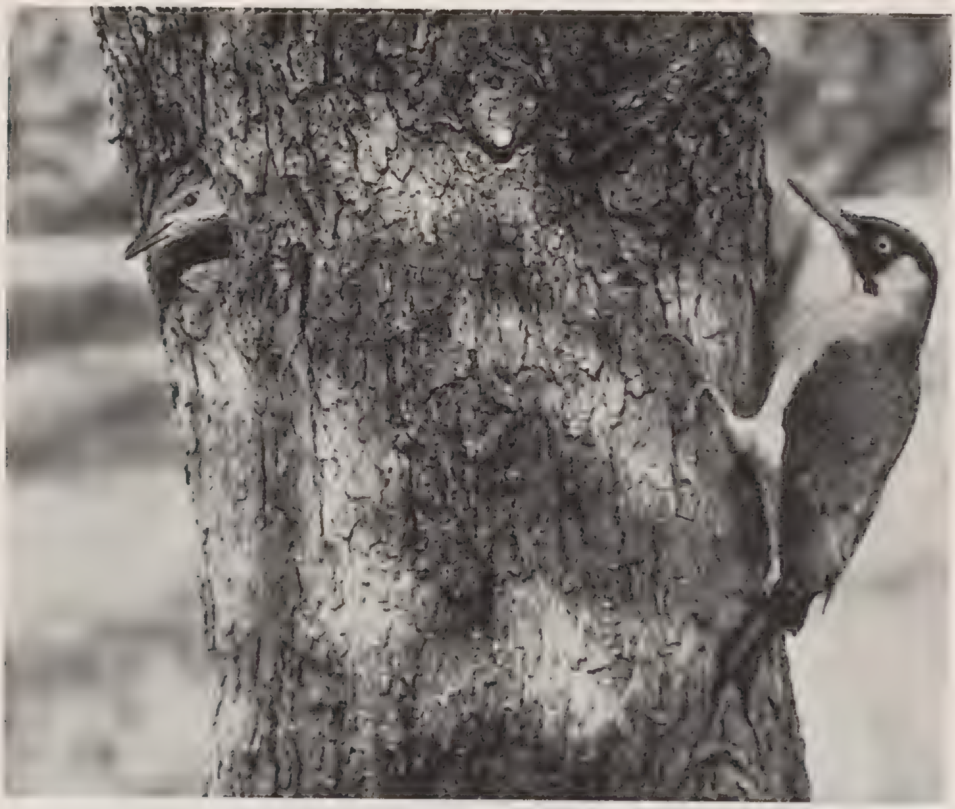


Photo by L. E. Day.

Fig. 2. Adult arrives, on opposite side of the tree, to the hole.

male as working 150 minutes on one occasion; the bird came to the mouth of the hole for rest with opened beak and protruding tongue, panting, but this was on a very warm day.

### *Feeding the young*

As soon as the young birds were sufficiently grown to move about inside the hole, they were fed from the outside. The adult came to feed at periods of 50 to 60 minutes at this stage. The male arrived first, usually alighting below or on the opposite side of the tree to the hole, jerked its way to the entrance, pointed the bill nearly vertically, and went through retching motions opening and shutting the mandibles rapidly whilst doing so. When still again, the mandibles were slightly apart and a mass of food was visible,

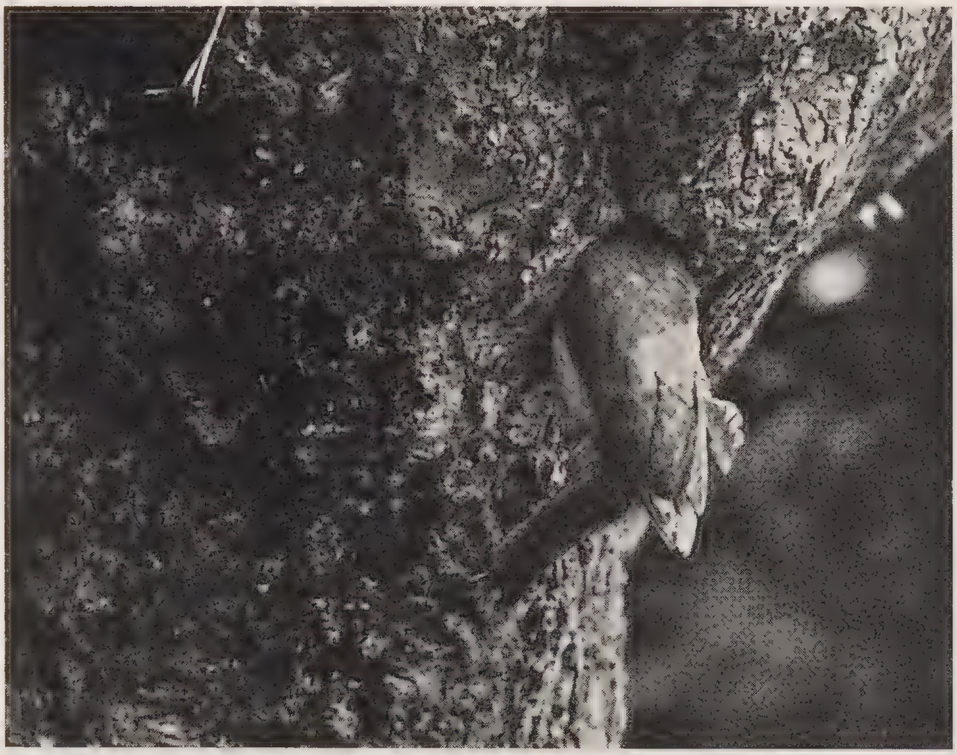


Photo by A. Mc. Cormick.

Fig. 3. The adult feeding a young one inside the hole after regurgitating outside. The tail is always tight against the bark unless the bird sits horizontally in the hole.

from about the middle to the base of the bill. The head was placed in the hole, the tail remaining tight against the bark, and the whole body and plumage of the bird was quivering. The head was withdrawn and the motions repeated. This was done six times, the same action being performed five times, but after the sixth retching, the bird sat horizontally in the hole, the hind half of the body and tail protruding and quivering. This last position was the only one where the tail was not against the bark for support. The bird then entered the hole, stayed a little while, and usually flew, without pausing at the entrance, to a nearby tree. Within a few seconds the female arrived, and went through a similar procedure to that of the male, regurgitating six times and feeding six times. Each adult was there from 2 1/2 to 3 minutes. When the female left the hole both adults flew away together. Usually a low call 'weet, weet' was given by one bird and an-

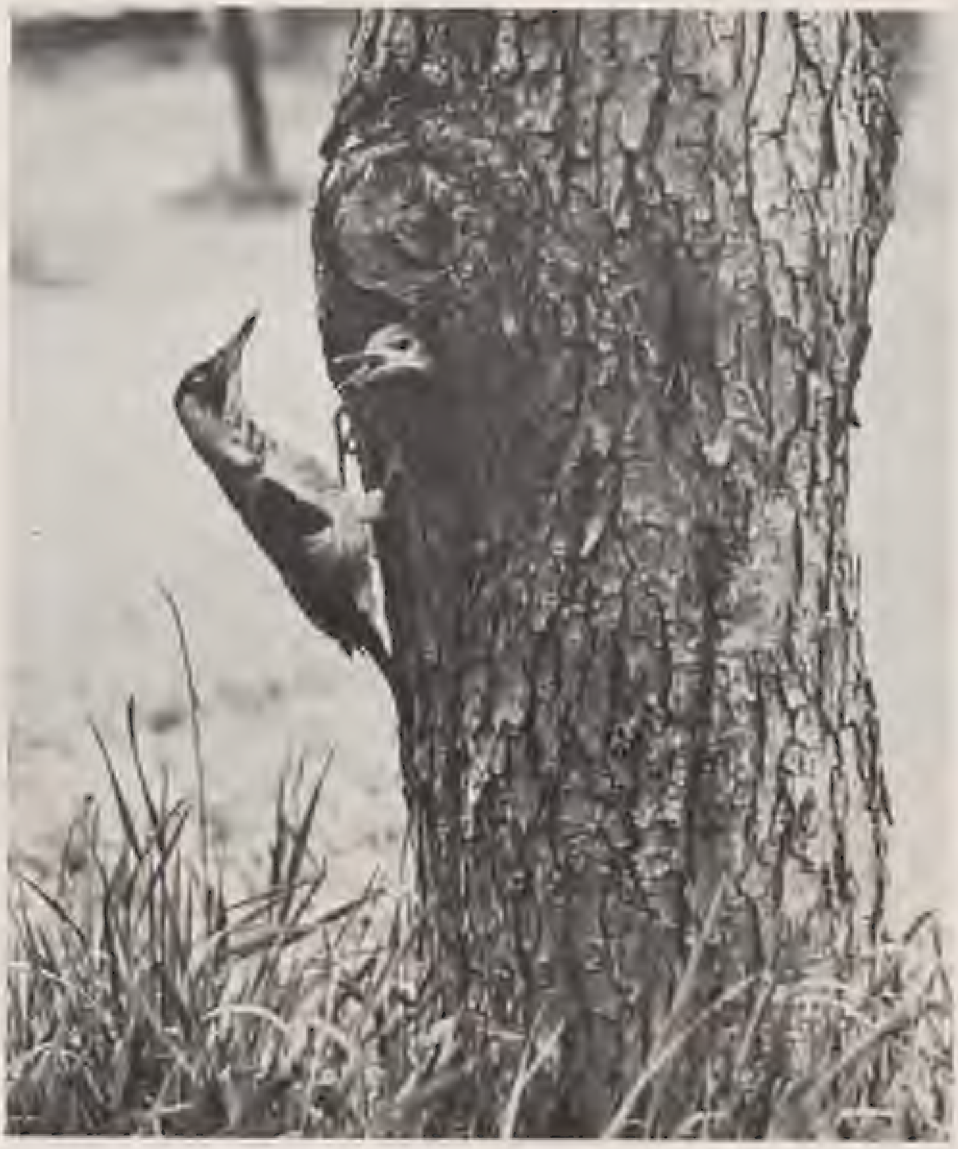


Fig. 4. Regurgitating. Photo by G. Lawrence.

swered by the other when they arrived to feed the young. Sometimes 3 or 4 retchings took place outside, the adult then entering. If further retching took place it was always done, out of view, inside the hole.

When the young were feathered, one head or another was out of the hole

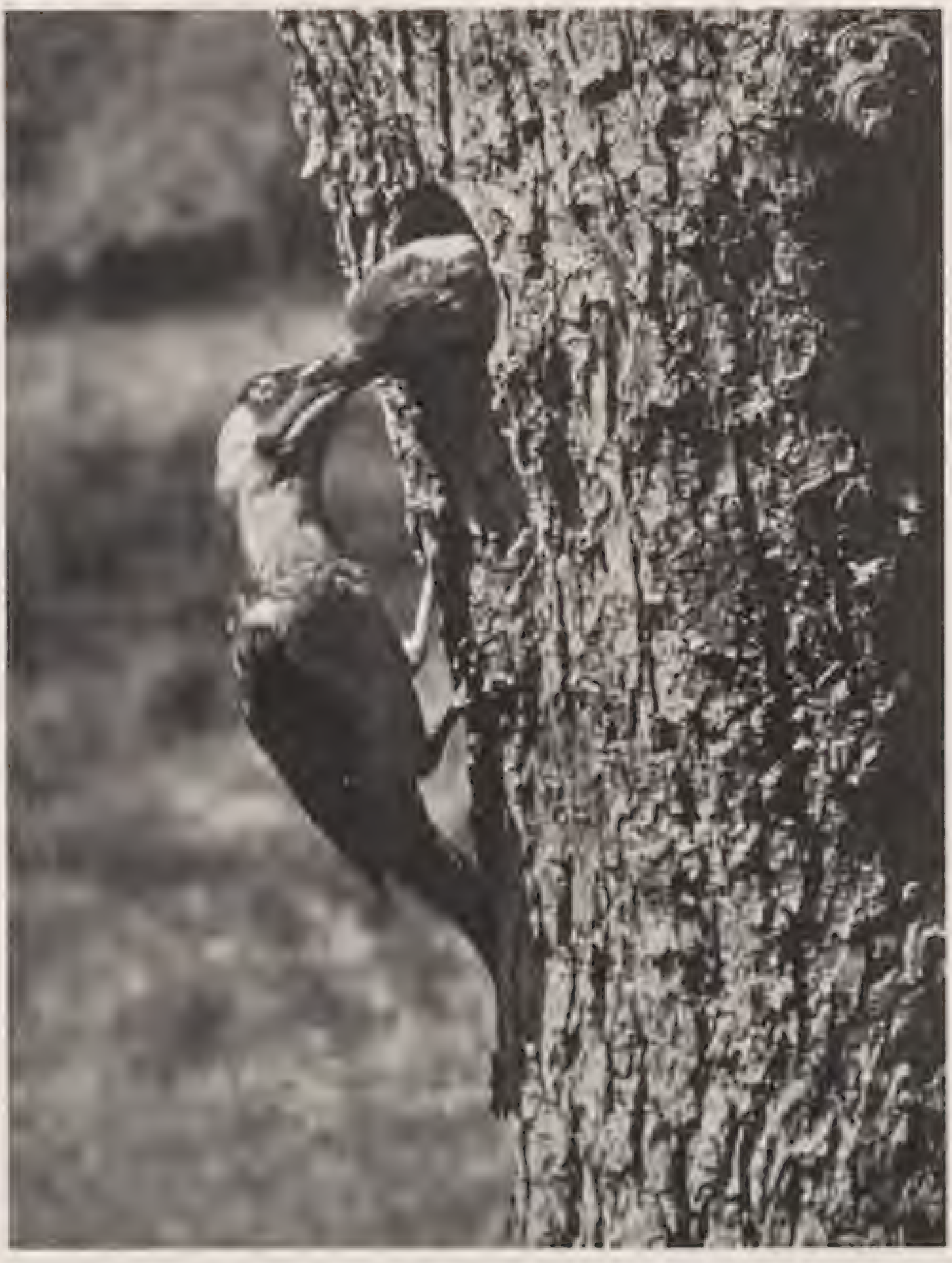


Photo by L. E. Day.

Fig. 5. The bills not quite fully engaged. The tip of the upper mandible of the young almost touches the eye when the food is passed and the heads move in unison backwards and forwards with a rapid motion.

almost all the time. There was a continuous squawking, harsh and raucous. It ceased when any person appeared and was intensified on the arrival of the parent birds.

The feeding was now visible most of the time. An adult came to the nest hole on one side or the other, retched food into the bill, turned the head so that the space between the mandibles was in a vertical plane; the youngster placed its mandibles above and below along the spaces, the tip of the adults bill, as the slides show, being well inside the mouth of the chick, and the points of the latter's mandibles almost to the eyes of the adult. The heads moved backward and forward a short distance, but with great rapidity, whilst the beaks were locked together, the whole plumage of the adult displaying a rapid quivering that was a counterpart to the movement of the heads. Sometimes four and sometimes five young were fed in this way, and the remainder with the adult's head in the hole, but the tail tight against the bark all the time. Edmund Selous (''Bird Life Glimpses'' pp. 214–9) says the tail is away from the bark when so feeding, but neither I nor my co-workers have ever seen it removed, except as stated above, when the bird sits horizontally in the hole.

The latest feeding of the young observed by me, was at 18.40 (G.M.T.), and although both birds were in the vicinity, neither had returned till my departure at dusk.

During the last two days that the young remained in the hole, feeding became irregular, the female feeding less and less frequently, and the male doing more and more of the work. It was now that I observed what I can describe only as a ''rest period.'' The male once flew past the nest tree and clung on a branch of the next tree and remained there for exactly 15 minutes, perfectly still, except that the head was moved at any unusual sound. The beak was at an angle of c. 45° to the horizontal. The male again took up such a position on the trunk of the nest tree the next day and remained in that position exactly 22 minutes. The bird fed the young after the rest on both occasions.

(Illustrated with photographs by L. E. Day, F.R.P.S., M.B.O.U., A. McCormick, and G. J. Lawrence, B.Sc.)

# The British Long Tailed Tit (Ægithalos caudatus roseus) How its Nest is Built

*Violet Maxse*

*Pulborough, England*

It is well known that the Long tailed tit builds a remarkable nest made of moss (Hypnum) lichen (cryptogamia) and hair. These materials form the outer covering. Once this covering is completed, a lining of interwoven feathers is made containing sometimes over 2 000 feathers.

I have been lucky enough to observe this bird constructing its nest and have recorded a few details with a camera.

Both worked equally hard at building and I never discovered which of the birds was cock and hen. Mr. Jourdain records that both birds incubate, so one cannot be certain even then.

The white lichen is brought in beakfuls and is scattered over the outside of the nest. Its sticky roots firmly establish themselves and form an important part of the nest construction. Beakfuls of green moss were always taken inside, and small threads of bark go also into the inside with the moss.

As a rule, however, the nesting material is always added to the top tim of the nest, and we now come to his method of securing his material into place. Each bird worked by sitting inside with his tail cocked up at the back; and on this occasion he brought a spider's nest of silk cocoon; he hooked this cocoon on to a head of white lichen on the outside of the nest, and pulled at it hard. The silk stretched like a piece of elastic rubber, and he fastened the opposite end on to a peg of white lichen on the opposite side of the nest. For a few seconds a tiny rope of silk hung across the cup of the nest. He picked it up near one end; passed it over the rim of the nest and the newly placed nesting material, and secured it round an inside "peg" of moss. Having got it there he stretches it again over the rim to an outside peg of lichen; then another stretch from an outside peg to an inside peg until the cocoon silk would stretch no further. Many times did I see the nesting material brought to the rim and fastened down by that method.

On one occasion the silk got twisted round his own tail while he was still

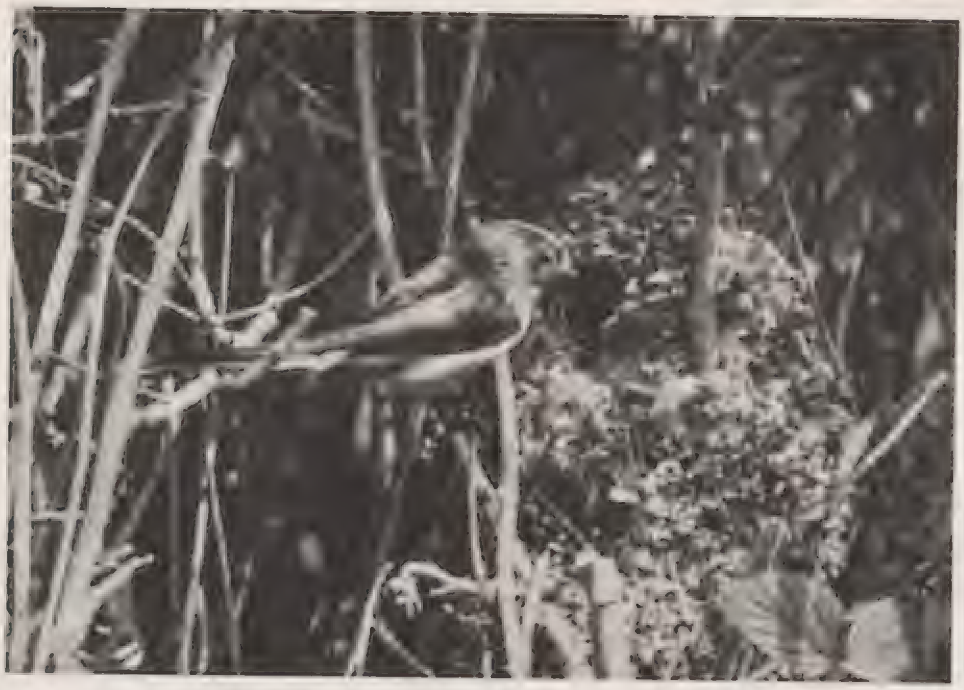


Fig. 1. The British long tailed tit — *Ægithalos caudatus roseus* — and his nest.

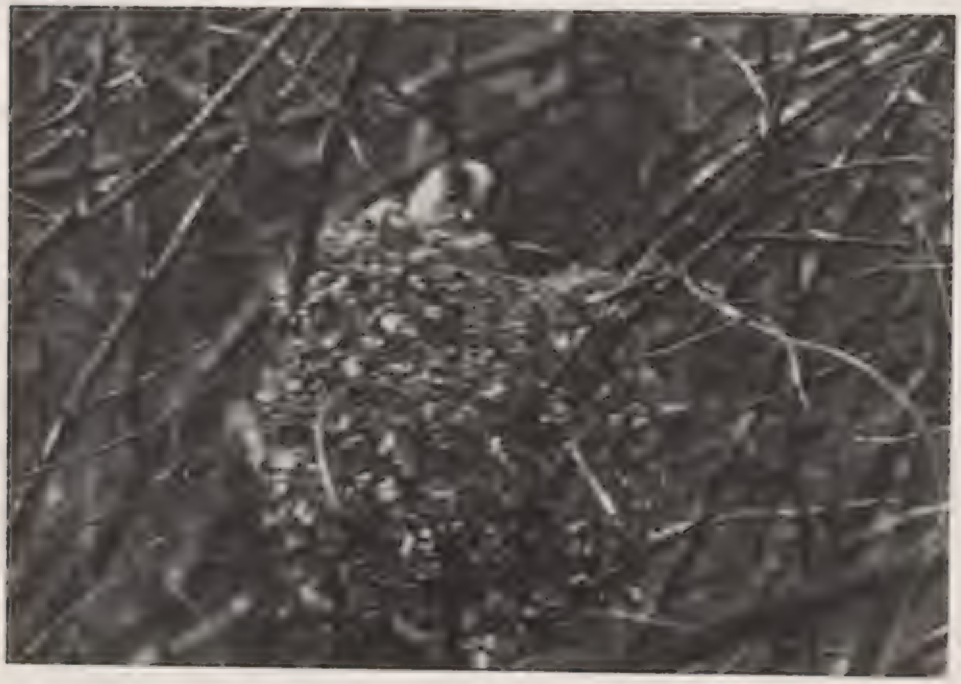


Fig. 2. The British long tailed tit — *Ægithalos caudatus roseus* — shaping his nest while building it.

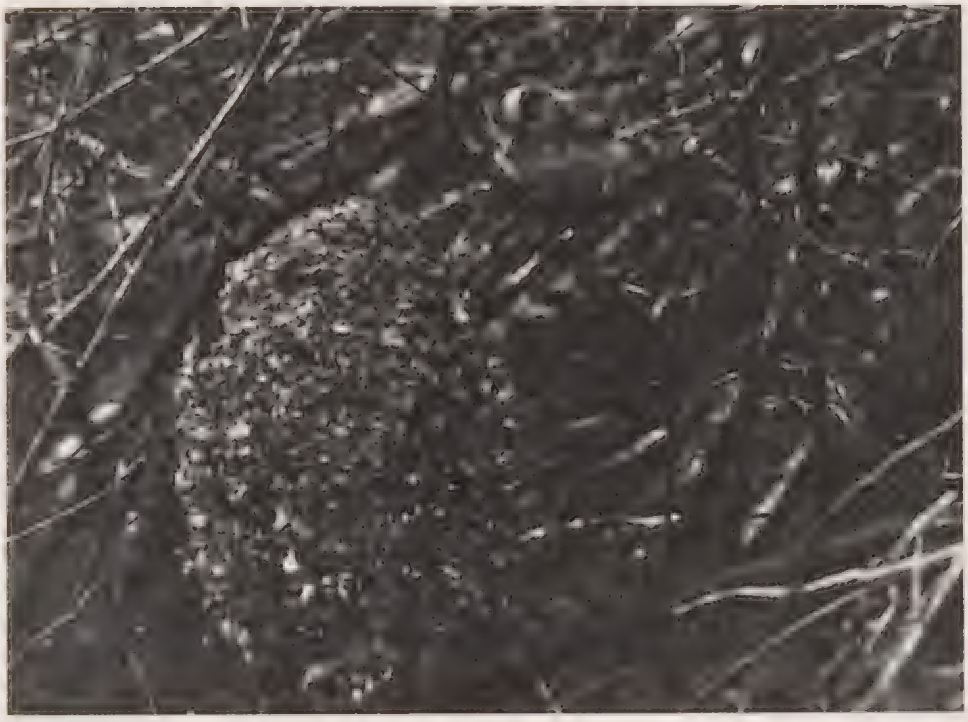


Fig. 3. The British long tailed tit — *Ægithalos caudatus roseus* — holding the end of Spider's "silk" he weaves into his nest.

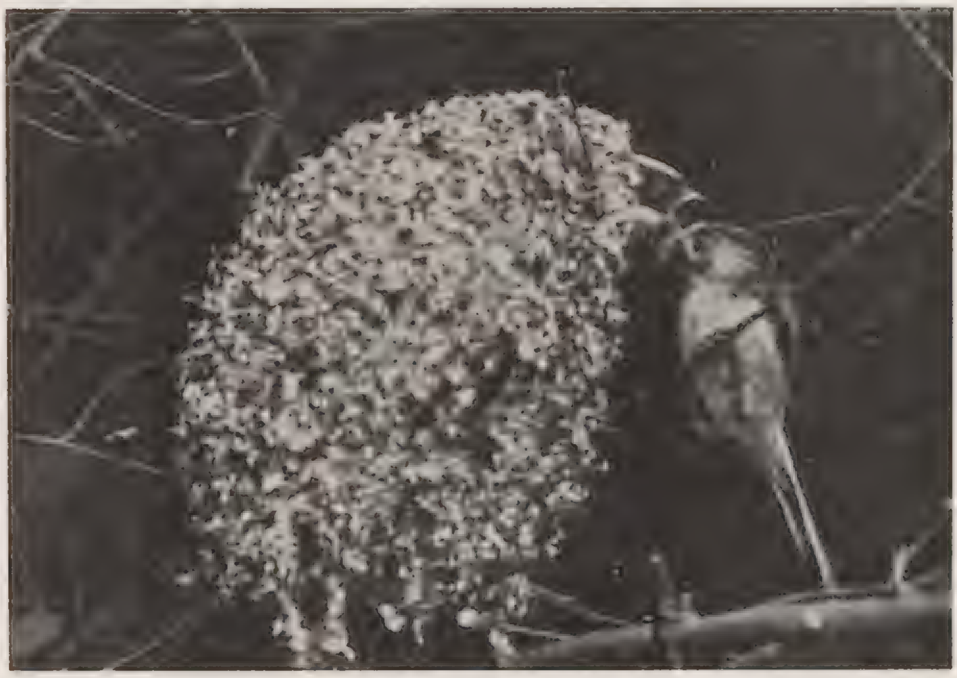


Fig. 4. The British long tailed tit — *Ægithalos caudatus roseus* — the fledgings on the day before they flew from the nest.

pulling at it. When trying to free himself his leg got entangled in it. Finally he had to fall over the outside of the nest and dangle on the silk until it broke.

It was equally important to get the nest the right shape. So he leant his chest against one wall (Fig. 2). He gripped the opposite wall with his claws; and he heaved the wall upwards with ceaseless backward kicking actions of his feet. The whole bush trembled as he "kicked" the wall upward two or three centimetres at a time.

When the roof was on and the feather lining was started I got a photograph of that spider's cocoon silk (Fig. 3).

Both birds arrived carrying feathers. One went in and his mate stayed outside. When the one inside came out he clumsily displaced the nesting material round the hole; he uttered a few notes to his mate. The mate looked at the damaged hole and took those feathers away. In a few minutes one of them was back again and picked up an end of cocoon silk; and immediately started to repair the hole.

The cock fed the hen (we suppose) while she was incubating and once brought a feather. Sometimes he would call to her and take her away for a while.

10 young birds flew from the nest, which contained 1 150 feathers.

*Discussion:*

R. Murphy congratulated the speaker on the care and scrupulousness of this brief but admirable study, and also on the clarity with which she was heard by everybody in the hall. He remembered that this had not always been true of the male contributors to the program.

# The black Cockatoo.

*E. J. L. Hallstrom*

*Taronga Zoological Park, Sydney*

In my talk on Black Cockatoos at Uppsala I purposely gave the talk as an Aviculturist having made a close study of these birds in the aviary and in their natural habitat.

When Captain Cook entered Botany Bay on the 28th April, 1770 in the sailing ship "Endeavour" and landed on the east coast of Australia—(the vessel also carrying Sir Joseph Banks, a famous naturalist of those times), one of the first birds he would have seen would be what is known to-day as the Glossy Black Cockatoo. These birds were very common, at that time, on the coastal areas surrounding Botany Bay, and, in fact, their food trees were very plentiful along most of the coast of New South Wales. This bird is smaller than the one we now know as the Banksian Cockatoo, and I remember, when I was a youth, seeing many Glossy Black Cockatoos in the area now known as Maroubra Bay, and just north of the entrance to Botany Bay. On several occasions I had seen Glossy Black Cockatoos in the exact area where Captain Cook landed. It was as a result of seeing the birds in these areas that I first became interested in them. They were very common around Sydney, and were shot in large numbers. The Banksian and the Glossy Black both for many years carried the name of Banksian (after Sir Joseph Banks). On close examination, however, the difference was found to be very marked, the Glossy Black being the smaller bird, very similar in the markings of the tail feathers, but carrying yellow, irregular feathers around the neck. Sometimes these feathers are orange coloured. Many years later the Glossy was re-named, and the larger variety of the Red-tailed Black Cockatoo retained the name of Banksian. It is most likely that the bird Sir Joseph Banks saw was not the Banksian, as we know it to-day, but in reality the Glossy Black.

Of the Black Cockatoos there are the Red-tailed, the Yellow-tailed and the White-tailed varieties. The many races of Black Cockatoos are distributed practically all over the Australian continent, as well as in Tasmania and Kangaroo Island, which adjoins the mainland.

There are many variations of Banksians. In Northern Australia the birds are very large, with an unusually large bill, and with much of the brilliant red blended with grey, and in parts very nearly white, with frequently a mixture of yellow, so that these birds have been frequently confused with the Yellow-tailed Black Cockatoo. In the Banksian varieties, the birds usually lay one egg, which they rarely fail to hatch. It would be impossible for me to say that the Banksian Cockatoo never lays more than one egg, but my observations are that I have never seen more than one. In an endeavour to peg the number of days required for incubation, I carefully watched a nest in my aviaries, checked the day the egg was laid, and found that the youngster hatched on the 29th day. To make sure of this I took a freshly laid egg, placed it in an incubator, and it hatched in the middle of the 29th day. In my aviaries, immediately after the young bird was taken away from its parents, they commenced breeding again, and I have a pair of Banksians that produced three nests, of one bird each, in the year. In the natural state the parents and the young bird remain together until the next breeding season. The Banksian Cockatoo, if taken from the nest, may be reared in a similar way to the White and Yellow-tailed varieties. In Central Australia and in Southwest Australia and New South Wales, the birds are smaller. In the western part of Australia a White-tailed variety is to be found and I have noted two types, both appearing very similar until closely examined. One has a very slender bill, while the bill of the other is thicker and more solid. As far as I know the habits of these two birds are very similar and may be local variations.

The White-tailed Black Cockatoo has lately been declared a pest, as it has formed a habit of destroying apples in search of the pips. Most Black Cockatoos, once they have been taught to eat apple pips, become very fond of them. This is a great pity as such a beautiful bird may become scarce and rare if shot to protect the apple orchards. They consume a large quantity of hard native nuts, also nectar-carrying blossoms and the soft bark and leaf buds of the eucalyptus tree. In captivity, they are very interesting and may be reared on boiled hulled oats, oatmeal porridge mixed with cream and sugar. When reared from the baby stage, they do quite well on a diet of one third sunflower seed, one third canary seed and one third peanuts or other nuts rich in oils. They may be given large grubs of which they are very fond. Lettuce and some green stuff may also be included. The difference between the sexes is that the beak is light in colour in the female. and black in the male. The female has a large clear white patch on the cheek, whilst in the male it is greyish coloured. The feathers of the females are mostly tipped with white, giving the birds a greyish appearance. The general colour of the male is blackish and not nearly as pretty as the female, With the Yellow-tailed Black Cockatoo the colouration is the same, with the exception that yellow replaces the white. Aged males of both these birds develop a pink or reddish wattle around the eye. The Yellow-tailed variety is found on the eastern coast of the mainland, Tasmania, South Australia and on Kangaroo Island. I have carefully checked on the breeding hollows of the Yellow-tailed Black Cockatoo, but have not had the opportunity to do so with the White-tailed, although I would expect they would be similar. I found some nests contained two eggs—some of the birds choosing only to rear one chick where two birds were hatched. Last year (1949) two nests were observed with two babies in each.

None of the Black Cockatoos is vicious, and if hand-reared very seldom bite, preferring to screech loudly and struggle to make their escape from one's hands without attempting to bite as an ordinary White Cockatoo or Corella would do.

They breed in the hollow trunk of a tree standing in an upright position. They build a nest of sticks. The sticks are about a foot in length, and the bird very carefully splits them from end to end, so that they have three or four carefully-split pieces of the original twig. The pieces are then placed in the hollow, making a nest on which the egg or eggs are laid. In the event of a heavy downpour of rain the nest is not swamped, as the bird has already chosen a hollow that has been cracked with age—this crack allowing the water to escape while the eggs remain dry on the nest of twigs.

Another very interesting Black Cockatoo is known as the Great Palm Cockatoo. It is found at the extreme north of the Continent on Cape York Peninsula. There is not a large population of the Great Palm, or as it is known locally, the Australian Macaw, on account of the bare patches on the face. This bird has a huge bill which it uses with great effect on the very hard-shelled nuts. It is also the possessor of a large crest of long, fine feathers.

In the wild state they are most amusing and interesting birds. They will stand on the high limb of a tree and stamp their feet when you approach, screeching with a very loud whistling note. The birds act as though they are clowns in a circus. In New Guinea the same bird is caught by filling in small salt pans with stones and leaves until only a small circle of salt water, not more than 9 inches across, is left. The birds visit these small holes and drink with relish the brackish water. After several days snares are set and the birds captured. Within a very short time they quickly become used to captivity, and some caught in this way only a year ago are building nests in my aviaries.

Turning back to the Glossy Black Cockatoo. This bird is particularly interesting as its feeding habits are very highly specialised. It eats seed from the cones of the casuarina tree, and its bill is specially adapted for that purpose, being broad and strong. I am sure that none of these Glossy Black Cockatoos had ever been reared in captivity until I reared one in 1946. I made several fresh attempts to rear these birds, only to realise that there was something different in their anatomy, and a post mortem revealed that the bird had not a gizzard as one would expect to find in other parrots. Close examination proved that inside the body and close to the crop was a receptacle containing food, which was not, however, a muscular gizzard. It is a parchment-like bag, and seemed very like a secondary crop for the storage of food. In one part of the intestine was found rudimentary muscles, not more than 1/16'' thick, similar to the gizzard muscles. It was noticed that a muscular portion of the bowel had apparently two valves, and the outer one became quite easily blocked when the bird was fed with any substance containing fine bran. The bran of rice, oats, groats or wheat would completely cause a stoppage. It, therefore, became necessary before attempting to rear this bird, to find a substitute for the soft, oily kernels of the Casuarina cones. I know of no other natural seed or substance that these birds will eat, and should at some time, moths which have already invaded the seed in some areas around Sydney, spread throughout the State, this lovely and interesting Australian bird must disappear, so far as its wild state is concerned. In the course of my investigations in regard to the Glossy Black Cockatoo, I eventually found a method of making a substitute food with which I have successfully reared the second bird.

Rearing any of these birds is a long task and takes over a year, if they are reared by hand, and the order in which I would place them is as follows:

(1) The Banksians are the easiest to rear by hand;
(2) The White-tailed variety;
(3) The Yellow-tailed. These birds are very difficult to rear, requiring very careful and continuous supervision.
(4) The Glossy Black.

The scientific names of these Black Cockatoos are:

| | | |
|---|---|---|
| The Banksian Cockatoo | *Calyptorhynchus* | *banksii* Latham |
| The White-tailed Cockatoo | » | *baudinii* Lear |
| The Yellow-tailed Cockatoo (Funereal) | » | *funereus* Shaw and Nodder |
| The Glossy Black Cockatoo | » | *lathami* Temminck |
| The Great Palm Cockatoo | *Probosciger* | *aterrimus* Gmelin |

*Calyptorhynchus magnificus* Shaw and Nodder has also been used for the Banksian Cockatoo, and the Australian form of the Great Palm Cockatoo would be called *Probosciger aterrimus macgillivrayi* Mathews.

# Der Rhytmus in den Brutzeiten einiger schweizerischer Vögel

*H. Noll*

*Basel*

Die Arbeit geht aus von der Frage: „Wie viele Bruten sind einer Vogelart möglich innerhalb einer Jahresfortpflanzungsperiode?" Die Tabelle gibt Auskunft. In ihr ist alles auf die Zeit bezogen, in welcher die Vogeleltern an die Brut gebunden sind, denn das allein ist massgebend für die Beantwortung der Frage. Eine Anzahl Begriffe mussten dazu neu gefasst oder gebildet werden.

Es bedeutet:

*Brutzeit*, die Zeit, während der die Vogeleltern mit einer Brut beschäftigt sind, also vom Nistbeginn an bis zum Selbständigwerden der Jungen, somit nicht mehr bloss die Inkubationszeit, hier Bebrütungszeit genannt. Die Brutzeit wird eingeteilt in Nistzeit, Bebrütungszeit, Aufzucht- und Führungszeit. Diese beiden letzten Zeiträume fallen bei den meisten Nestflüchtern zusammen, bei den Nesthockern sind sie in der Regel getrennt. (Siehe Stockente und Rauchschwalbe.)

*Brutzeitbreite* ist der Zeitraum innerhalb dessen Bruten mit Erfolg aufgebracht werden können, also von der ersten Nistbeobachtung einer Art innerhalb der Jahresfortpflanzungsperiode bis zur letzten Beobachtung der Führung von Jungvögeln.

Die Zahlen unter den Brutzeitbreiten bedeuten die späteste Schlüpfzeit für sichere Aufzucht der betreffenden Art. Rein rechnerisch lässt sich also die Zahl der möglichen Bruten einer Art innerhalb der Jahresfortpflanzungsperiode finden nach der Formel:

$$\frac{\text{Brutzeitbreite in Tagen}}{\text{Brutzeit in Tagen}} = \text{Zahl der möglichen Bruten.}$$

Wenn trotzdem mehr Bruten stattfinden ist dies nur möglich, weil

a) die Bruten ineinandergeschachtelt werden durch Arbeitsteilung der Vogeleltern z. B. Amsel:

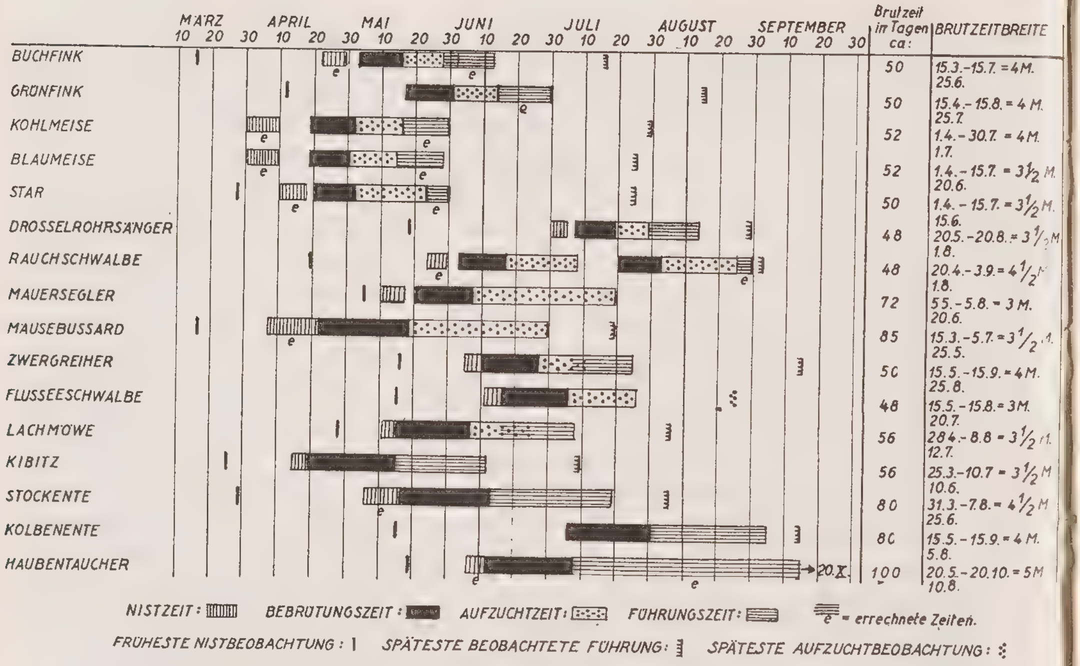


Fig. 1. Brutzeit und Brutzeitbreite einiger schweizeriger Vögel.
Weitere Figurerklärung siehe Text.

♀: baut, brütet und füttert

♂: füttert hauptsächlich und führt die Jungen = Einsparung der Führungszeit

b) durch Einsparen der Nistzeit, indem das alte Nest benützt wird (Rauchschwalbe).

Zu dieser Brutzeitbreite fehlt noch die Zeit, die eine Vogelart in ihrem Jahresrhythmus braucht, um die erloschene Fortpflanzungsfähigkeit wieder zu gewinnen. Sie könnte als ,,Brautzeit'' bezeichnet werden, ich möchte eher ,,Zwischenpubertätszeit'' vorschlagen. Sie muss nach äusseren Erscheinungen bestimmt werden die mit dem Geschlechtsleben in Zusammenhang stehen, für Singvögel z. B. die Zeit des Gesangsbeginnes bis zur ersten Nistbeobachtung. Für die Zugvögel unter ihnen ist die Methode allerdings nur für früh einrückende Arten verwendbar, da wir bei später einrückenden nicht sicher sind, ob sie nicht schon gepaart ankommen (s. Tabelle).

Für Nicht-Singvögel scheinen mir die ersten Anzeichen der Balz, der Werbe- und Liebesspiele, die freilich eher noch Gesellschaftsspiele sind,

| Art | Gesangsbeginn | Erste Nistbeobachtung | Zwischenpubertätszeit |
|---|---|---|---|
| Amsel (*Turdus merula* L.) | 17. Febr. (Mittel aus 31 Jahren) | 20. März | 31–(34) Tage |
| Buchfink (*Frigilla coelebs* L.) | 14. Febr. (36 J.) | 15. März | 29-(31) Tage |
| Kohlmeise (*Parus major* L.) | 22. Jan. (27 J.) | 27. März | 64 Tage |
| Star (*Sturnus vulgaris* L.) | 20. (23.) Febr. (24 J.) | 29. März | 34–37 Tage |
| Sumpfrohrsänger (*Acrocephalus palustris* Bechst.) | 25. Mai (Ankunft 24. Mai) (9 J.) | 6. Juni | 12 Tage |

die besten Merkmale für das Wiedererwachen der Geschlechtstätigkeit zu sein. Bei den Zugvögeln unter ihnen wären vielleicht die ersten Balzhandlungen nach der Ankunft massgebend. Beispiel:

Lachmöve (*Larus ridibundus* L.)

| | |
|---|---|
| Erste Besuche des Brutgebietes | 15. März |
| Frühester Nistbeginn | 28. April (20.4.49) |
| Zwischenpubertätszeit | 36-(44) Tage |

Für Enten, z. B. unsere Stockente (*Anas platyrhynchos* L.) ist die Zwischenpubertätszeit besonders schwierig zu bestimmen. Ihre Verlobungszeit fällt in den Herbst. Es sind richtige Werbespiele damit verbunden. Dann setzt die Periode wieder aus, erst Anfang März beginnt die eigentliche Reifezeit, die etwa 30 Tage dauert.

Aus den angegebenen Zahlen und Daten geht hervor, dass die Zwischenpubertätszeit wie auch die Brutzeitbreite nach Zeitdauer und Zeitlage für jede Art und für eine bestimmte Gegend konstant sind, also ein Rasse- und Artmerkmal im weiteren Sinn bedeuten.

# Vom Brutvogelbestand eines Hochgebirgswaldes im Wallis

*A. Schifferli*

*Vogelwarte Sempach, Schweiz*

In den Jahren 1948 und 1949 taxierte ich im Lötschental, im obern Teil des Kantons Wallis, im Mai und Juni den Brutvogelbestand einiger Lärchenwälder. Der Lärchenwald, von dem ich hier berichte, liegt am Fluss Lonza, 1800 m ü. M. Er misst 7–8 ha und setzt sich aus verschiedenaltrigen Lärchen (*Larix*) zusammen; die ältesten unter ihnen dürften über 200 Jahre alt sein. Um das Hotel, in Waldesmitte, stehen wenige Fichten, gegen die Lonza hin wachsen einige Erlenbüsche. Die Lärchen stehen recht locker und geben dem Wald einen parkartigen Charakter. Sein Boden ist mit Heidelbeersträuchern, Kräutern und Gras bewachsen.

Für meine Bestandesaufnahmen kartierte ich in den frühen Vormittagsstunden im Mai und Juni die singenden Vogelmännchen. Meist fand ich später auch die zugehörigen Weibchen und oft auch die Nester, sodass ich mit grosser Sicherheit den Brutbestand in diesem Wäldchen lückenlos erfassen konnte.

Im Jahre 1948 brüteten wenigstens 94, im Jahre 1949 wenigstens 83 Singvogelpaare in je 16 Arten (siehe Kartenskizze). Daraus ergibt sich die erstaunliche Dichte von rund 120 Paaren auf 10 ha Lärchenwald. Es wird damit die obere Besiedlungsdichte schweizerischer Mittelland-Wälder erreicht. So fand F. Amann in einem 10 ha grossen Laubwald von Eschen, Eichen und Hagebuchen bei Basel 120–130 Brutvogelpaare. Die Fringilliden, *Fringilla coelebs, Carduelis flammea* und *C. citrinella* dominieren auf der Fafleralp mit 66 beziehungsweise 63 %. *F. coelebs* ist der häufigste Vogel, 43 beziehungsweise 49 % des Gesamtbestandes für 1948 und 1949 entfallen auf diese Art.

Der Brutvogelbestand blieb in den beiden Jahren konstant, nur bei *F. coelebs* sank er im Jahre 1949 von 46 auf 36 Paare.

Im Walde suchten sich die einzelnen Arten ihre typischen Biotope. Die Fringilliden verteilten sich gleichmässig. *Anthus trivialis* bevorzugte den

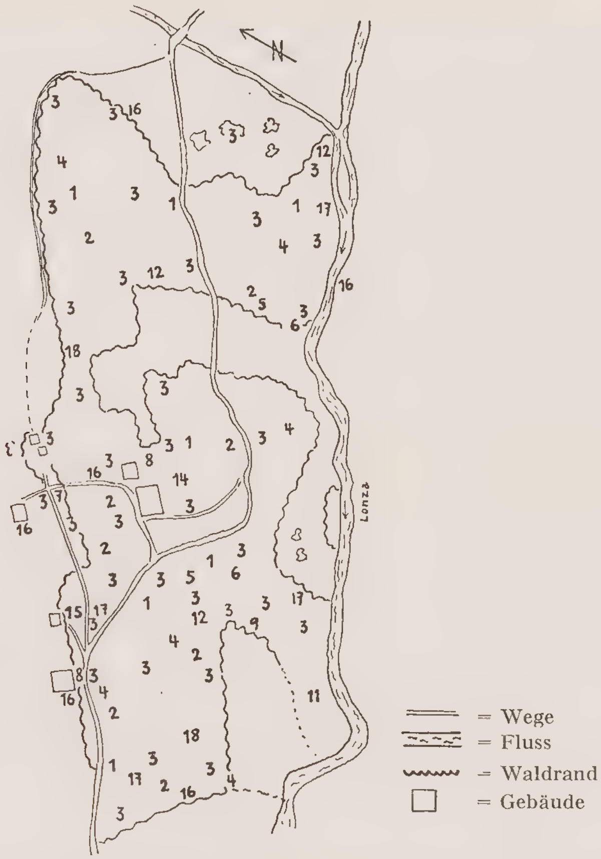


Fig. 1. Der Brutvogelbestand eines Lärchenwaldes im Lötschental im Mai und Juni 1948 und 1949. Die Ziffern beziehen sich auf untenstehende Arten.

| | Anzahl 1948 | Paare 1949 | | Anzahl 1948 | Paare 1949 |
|---|---|---|---|---|---|
| 1. Carduelis flammea | 8(10) | 8(10) | 10. Muscicapa striata | — | — |
| 2. Carduelis citrinella | 8(10) | 8(10) | 11. Sylvia borin | — | 1 |
| 3. Fringilla coelebs | 46 | 36 | 12. Turdus viscivorus | 2(3) | 3 |
| 4. Anthus trivialis | 6 | 6 | 13. Turdus ericetorum | —(1) | — |
| 5. Certhia familiaris | 2 | 2 | 14. Turdus torquatus | 1 | 1 |
| 6. Parus ater | 3 | 2(3) | 15. Phoenicurus phoenicurus | 1 | 1 |
| 7. Parus cristatus | 1 | 1 | 16. Phoenicurus ochruros | 6 | 5(6) |
| 8. Parus atricapillus | 2 | 2 | 17. Prunella modularis | 4 | 4 |
| 9. Regulus regulus | 1 | 1 | 18. Troglodytes troglodytes | 2 | 2 |
| | | | | 93 | 83 |

Rand, *Phoenicurus ochruros* die Nähe von Gebäuden und Blockfeldern, *Regulus regulus* die wenigen Fichten, *Turdus torquatus* ebenfalls, während *T. viscivorus* im Gegensatz zu *T. torquatus* auch das Nest für die 1. Brut auf Lärchen machte. *Prunella modularis* und *Troglodytes* nisteten in den schattigen Waldteilen.

Es sollen ganz kurz einige Probleme gestreift werden, die sich auf die Bestandesdichte beziehen.

Entsprechend der grossen Zahl der brütenden *F. coelebs*, ist deren Brutterritorium klein. Die Nester fand ich oft kaum 20 m von einander entfernt. Kämpfe zwischen ♂♂ und auch Paaren waren häufig. Nistmaterialtragende ♀♀ wurden öfters von fremden ♂♂ verfolgt. *C. flammea* und *C. citrinella* rissen hin und wieder Nistmaterial aus Nestern von *F. coelebs* und wurden wohl deshalb von letzteren vertrieben, sobald sie sich in Nestnähe zeigten. In 80 % der kontrollierten Nestern von *F. coelebs* — es waren deren ungefähr 20 — fand ich nur vier Eier als Vollgelege, währenddem im schweizerischen Mittelland Fünfergelege die Regel bilden. Es scheint mir wahrscheinlich, dass die grosse Bestandesdichte und die damit verbundene Nahrungskonkurrenz kleinere Gelege bevorzugen. Dazu kommt noch, dass im Mai und Juni, also zur Brutzeit, die Nächte auf 1800 m Höhe recht kalt sein können. Temperaturen bis —6° C sind keine Seltenheit. Erst zwischen 6 und 7h, wenn die Sonne die Hänge bescheint, verschwinden die Rauhreife und das Insektenleben erwacht. Die Tageszeit zum Futtersuchen ist somit für *F. coelebs* um 1–2 Stunden kürzer als im Unterland. Doch sind weitere Beobachtungen notwendig, um die Zusammenhänge von kleinerer Gelegegrösse bei *F. coelebs* nahe der oberen Baumgrenze klar aufdecken zu können.

Der Bestand von *F. coelebs* war im Jahre 1949 etwas kleiner als im Vorjahre. Möglicherweise ist die Abnahme auf den zweimaligen starken Schneefall im Juni und Juli 1948 zurückzuführen. Mehr als zwei Drittel der 1. Brut und der folgenden Nachgelege gingen damals zu Grunde. Als während 2–3 Tagen 20 cm hoch Schnee lag, benötigte *F. coelebs* ein Vielfaches der normalen Zeit, um den Kropf mit Insekten für seine Jungen zu füllen. Die Eier oder Jungen erkalteten während der lange dauernden Abwesenheit des ♀ und starben.— Die beiden *Carduelis*-Arten dagegen holten sich Löwenzahnsamen weiter unten im schneefreien Tal und kehrten damit in kurzer Zeit wieder zu ihren Nestern zurück. Ein Ausfall an Jungen trat deshalb nicht oder wenigstens nicht im selben Masse wie bei *F. coelebs* ein. Ihr Brutbestand blieb denn auch 1949 unverändert.

Zum Gesamtvogel-Bestand müssen wir uns noch fragen, wie ein Lärchenwald auf 1800 m Höhe, kaum 400 m unterhalb der oberen Baumgrenze, soviele Vogelpaare mit ihren Jungen ernähren kann, wenn zu Brutbeginn im April und anfangs Mai der Waldboden und die umliegenden Wiesen noch mit Schnee bedeckt sind.— Unablässig sieht man zu dieser Zeit *Parus*- und *Carduelis*-Arten in den noch nadellosen Lärchenzweigen umherturnen und kleine Insekten abpicken. Auch *F. coelebs* frisst ausgiebig von dieser Nahrung. Es handelt sich dabei um die überaus häufige, flügellos überwinternde Blattlaus *Chermes strobilobius,* die mit ihren Eipaketen auch von den andern Vögeln, wenn auch nicht in diesem Ausmasse, verzehrt wird. Diese Blattläuse bilden die hauptsächlichste Nahrung für die Fringillidae und die Paridae zu Beginn der Brutzeit. Es ist deshalb anzunehmen, dass die grosse Brutvogeldichte in diesem Lärchenwald, — sie war in den umliegenden, ebenfalls taxierten, Lärchenwäldern ähnlich, — im Zusammenhang mit der Häufigkeit dieser Blattlaus steht.

*Diskussion*:

A. v. Vietinghoff-Riesch: Die Siedlungsdichte insektenfressender Vögel ist im allgemeinen unabhängig von der dargebotenen Menge an Nahrung und ist ein psychophysischer Faktor; das Minimum an Nahrung ist beinah überall vorhanden, trotzdem besiedelt der Vogel den einen Biotop dichter, den anderen dünner. Spinnen kommen aber auf allen terrestrischen Biotopen in genügender Zahl das ganze Jahr über vor und würden allein schon einer grösseren Siedlungsdichte als Nahrungsreservoir genügen. Nur in seltenen Fällen kommt es vor, dass eine Vogelart auf Vermehrung ihrer Nahrungsobjekte mit einer Dichtersiedlung antwortet (*Dendrocopus major pinetorium* und *Fringilla coelebs* in Revieren, die von Nonne (*Liparis monacha*) befallen waren.

# Ecological Relationships of the Guillemots Uria aalge and Uria lomvia

*D. E. Sergeant*

*Cambridge, England*

## Introduction

The purpose of this communication is to give a picture of the ecological relationships existing between two closely related species of gregarious seabirds. These are the two guillemots, or murres, *Uria aalge* and *Uria lomvia*, forms of which occur in the North Atlantic and Pacific Oceans. In both seas *aalge* is the southern species, *lomvia* the northern; but there is a relatively wide belt where they breed together.

In 1948 I was fortunate enough to be able to visit Bear Island in the Barents Sea and to study one of these mixed colonies of great size. It was strikingly seen that the two species did not mix completely at the breeding ledges, nor did they separate entirely, except at the margins of the colonies. This interesting state of affairs, which had been noted briefly by previous observers, contrasted with the ecological isolation usually found between closely related species of landbirds. Moreover it seemed a relatively simple ecological picture, the entire relation of the bird to the land being its choice of a nesting ledge.

Thus although I have not since this time been able to visit any other mixed colony of guillemots, I have looked more closely at Scottish colonies of *Uria aalge* and other auks, and have also examined some of the relevant literature. Moreover several observers, of whom I should like to thank particularly Dr. Finn Salomonsen, Mr. James Fisher and Dr. F. Gudmundsson, have very kindly given me details about colonies in Iceland and Greenland. Needless to say I should welcome further information helping to make this study more complete.

## Geographical Relationships

These are summarised on the accompanying maps (Fig. 1 and 2). It may be noted that *aalge* in both seas breeds north roughly to the limit of permanently open water; *lomvia* to the limit of water open in summer. Thus

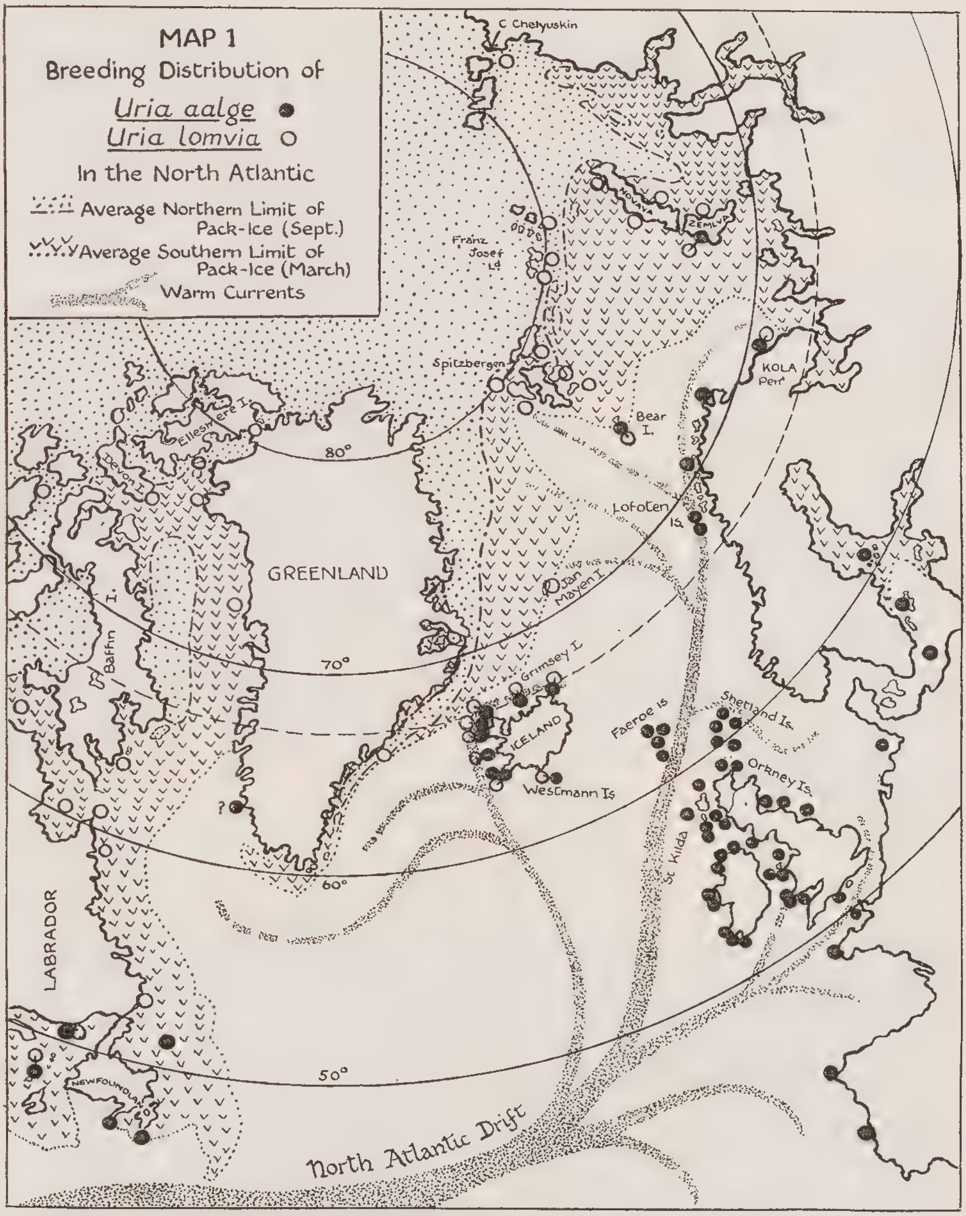

MAP 1
Breeding Distribution of
Uria aalge ●
Uria lomvia ○
In the North Atlantic
Average Northern Limit of Pack-Ice (Sept.)
Average Southern Limit of Pack-Ice (March)
Warm Currents
C Chelyuskin
Franz Josef Ld
NOVAYA ZEMLYA
Spitzbergen
Bear I.
KOLA Pen
Lofoten Is.
Ellesmere I.
Devon I.
80°
GREENLAND
Jan Mayen I.
Baffin I.
70°
Grimsey I.
ICELAND
Westmann Is
Faeroe Is
Shetland Is.
Orkney Is.
St Kilda
?
60°
LABRADOR
NEWFOUNDLAND
50°
North Atlantic Drift

Fig. 1.

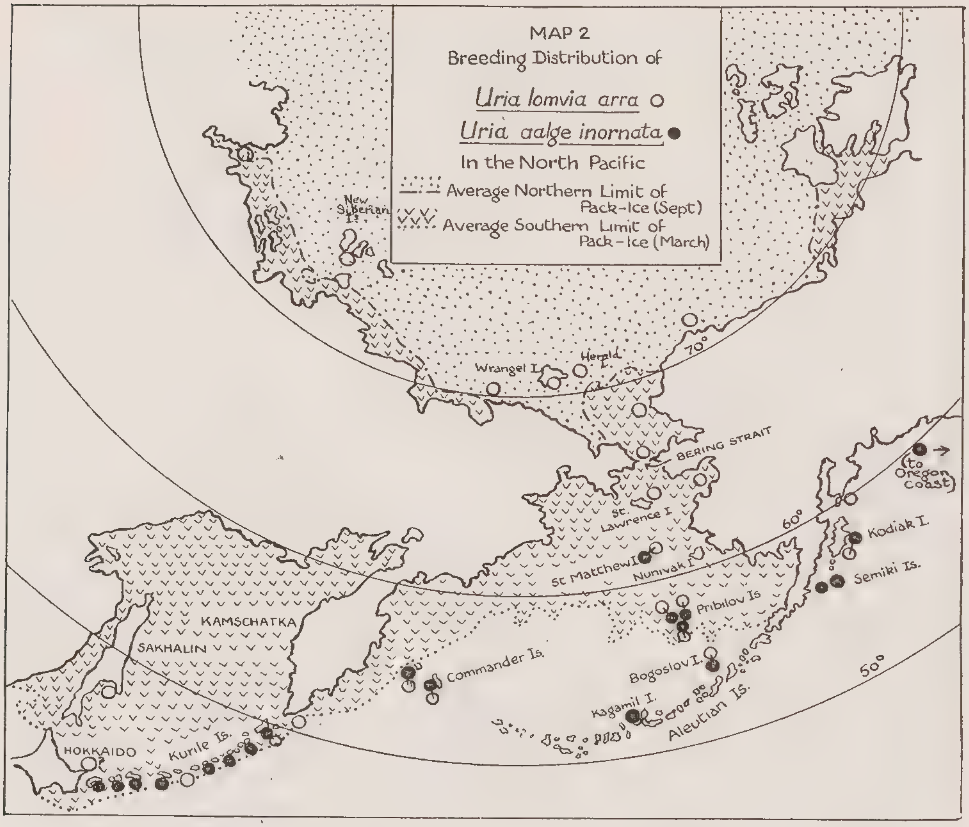


Fig. 2.[1]

the ranges follow, in a general way, the surface water isotherms; *lomvia* extending south in the Western Atlantic to Bird Rock in the Gulf of St. Lawrence, and in the Western Pacific to the Kuriles. *Aalge* in the Eastern Pacific has isolated colonies off the coasts of Oregon and California, where cold currents well up. (See map p. 280 in Steinbeck and Ricketts, 1941.)

The species breed together in the Atlantic at Bird Rock (Bent 1919) in south-west Greenland (Salomonsen, pers. comm.); all Iceland; Bear I., and Novaya Zemlya (Gorbunov 1925). In Iceland there is a transition from dominant *aalge* in the south, as at the Westmann Is., to dominant *lomvia* in the north at Grimsey (3/1 here in 1949, Foster et al., 1951); in the Pacific at the Commander Islands (Stejneger 1885), some of the Aleutians (Bent 1919), the Pribilovs (Bent, etc.), the Kuriles (Yamashina 1931), St. Matthew I., St. Lawrence I., and islands in Norton Sound (T. J. Cade, in litt.).

---

[1] Additional data, received since this paper went to press, extend the range of *Uria aalge inornata* north to St. Lawrence Island, and islands in Norton Sound, where the map shows only *Uria lomvia arra.*

The 'bridled' or 'ringed' mutant of *aalge* is known only in the Atlantic populations, where it increases in percentage northwards. (See Southern and Reeve 1941)

We may assume that the two guillemots were once a common stock that became separated into northern and southern forms, reproductively isolated, by some climatic barrier associated with the Pleistocene glaciations. As Salomonsen (1944) has clearly shown, *aalge* now exists as a chain of partly intergrading, partly isolated subspecies which follow the rule of Bergmann in becoming larger, and that of Allen in having the shorter bill, further to the north. Moreover the colour of the upper parts changes from a warm brown to almost black. In all these characters it comes to resemble *lomvia*. At Bear Island also, many birds in the field showed a faint white line (instead of a black) along the base of the upper mandible; *lomvia* has a clear white line. However, there is no suggestion of hybridisation between the two at this colony; one can tell even the chicks apart by the difference in the form of the bill. This total reproductive isolation exists even though the eggs and chicks become quite mixed up on the ledges upon human disturbance.

## Ecological Relationships

### *Breeding Ecology*

It does not appear that bridled *aalge* differ at all from typical birds in their breeding habits, though they do seem to group together at times in excess of random (Southern, pers. comm.). This may be the outcome merely of conservatism in breeding; the observations of Johnson (1941) make it seem highly probable that birds return year after year to the same ledges. Bridled *aalge* do not appear to associate preferentially with *lomvia*, as Hachisuka (1927) was informed.

Comparison of data from many colonies showed that the two guillemots have slightly different habitat preferences.

Thus at Bear Island, both were associated freely together on the long, regular dolomite ledges of the high southern cliffs, in a ratio of about one *lomvia* to two *aalge*. However, on the very edge of the clifftops *lomvia* occurred alone in a band, while on the flat tops there was a pure association of *aalge*. *Lomvia* was again dominant on the smaller, more irregular sandstone cliffs in the north of the island, where the ledges are on the whole smaller.

In Iceland an almost exactly comparable picture is given me by Gudmundsson for the north-east mainland colonies, and by Fisher for the Westmann Islands. On Grimsey, accurate counts show *lomvia* to outnumber *aalge* on the steep cliffs by 10/1, but on the least steep by only 2/1; this is apparently an expression of the difference in ledge-type. (Foster et al., 1951.)

At Novaya Zemlya there are only about 100 *aalge* in the large colony (estimated at 1 600 000 guillemots) at Bezymiannaya Bay, and these are all on the top ledges (Gorbunov 1925). On Bird Rock both species are together on the smaller sandstone ledges, but here all the larger ones are occupied by Gannets (*Sula bassana*) (Bent 1919). Gannets are always liable to oust guillemots where the two compete for ledges and flat tops, as at Cape St. Mary, Newfoundland (Keynes, pers. comm.) and Eldey, Iceland (Roberts, 1934). There is, however, no space here to deal further with the relations between guillemots and other species of seabirds.

In the Pacific a similar picture is given for Bogoslov Island in the Aleutians; but at Walrus I. in the Pribilovs there is clearly a greater separation into groups. This island has been fairly well visited over the last 60 years, and it appears that the relative proportions of the two species have changed from time to time, although some of the observers may not have covered the island adequately. Thus Palmer (1899) and Bent (1919) reported the Californian Murre more numerous, whereas since 1940 at least, Pallas' has been in exclusive possession (Gabrielson 1944, Kenyon through Bertram, pers. comm.).

There is a suggestion also of relative changes in the Kuriles, *aalge* having become more widespread and *lomvia* more restricted northwards between 1870 and 1930 (Yamashina, 1931). However, on Bear Island there is no evidence of any change, at least between Jourdain's visit of 1921, Bertram and Lack's in 1932, and the writer's in 1948. In no case, however, have we any quantitative data for comparison.

To sum up these habitat differences, one may say that *aalge* prefers flat places and crowds, and avoids crevices; while *lomvia* is less rigid in its choice of nest-site. Thus in the high arctic, where it occurs alone, *lomvia* breeds on all types of cliff-sites. In the south, *aalge* occurs on the same cliffs with the razorbill (*Alca torda* L.) at Atlantic colonies. Here the razorbill nests generally in crevices and on small ledges large enough for only one or two eggs; *aalge* generally on larger ledges in bigger groups, though there is a good deal of mixing. *Aalge* is always in open situations, and the crux of the habitat difference seems to lie in a difference of behaviour; *aalge* always broods its eggs standing upright, the razorbill habitually lying prone, and *lomvia* in either position. One would expect the razorbill and *lomvia* therefore to compete for nest-sites; the geographical overlap is mainly in Iceland, and here there is some evidence of segregation, for counts at Grimsey (Foster et al., vide supra) show that the main numbers of the two species are separated on extreme cliff-types. The two guillemots, on the other hand, merely separate out on the marginal habitats of the cliffs; *aalge* appears to have a slight selective advantage (? earlier arrival at the ledges) on the flat places, and will spread to the flat tops if they are safe from predators.

Only on Walrus Island does there seem to be an approach to all-or-nothing domination by one species or the other (vide supra), and here the birds nest over the whole island, so that nesting space may really be limited. I suggest that the intensity of interspecific competition for nest-sites is low for this main reason; the birds are social, each with a very small territory (no more than the area round the egg defendable by the sitting bird), and have no other demands on the land. Thus there is rarely shortage of *Lebensraum*, and the mixed colonies remain more or less permanently. Moreover, this social habit extends to the feeding. This thesis must now be developed.

## *Feeding Ecology*

An attempt at comparison of the diets of the two species showed that data were inadequate in any area where the two occurred. At Bear Island in July—August 1948, both fed principally on small gadoid fish. Published data (see esp. Cottam 1936, Hartley and Fisher 1936, and Witherby, 1941) show that both species feed principally on fish, *lomvia* often to a large extent on planktonic crustacea also, unlike *aalge*. However, these are more abundant in arctic than in temperate surface waters.

In any given area, it is probable that the pelagic-feeding seabirds take the most abundant food animals available, and concentrate in water-bodies where these are most dense. Thus at Bear Island, guillemots, skuas and especially fulmar petrels (*Fulmarus glacialis*) were taking an unidentified polychaete worm in large numbers; at Icefjord in Spitsbergen many species were feeding on the euphausiid *Thysanoessa inermis* and other crustacea at the foot of a glacier (Hartley and Fisher, vide supra.) Here we have an example of a localised feeding ground; I have noted, also, at Bear Island and in the Hebrides, the tendency of guillemots to fly in long strings to and from a particular feeding ground, evidently a concentration of fish.

For such species of birds, feeding far from their nesting sites, it will be a collective advantage to be gregarious in feeding, since the constant procession of birds keeps the feeding ground (which may be shrouded in fog) located for others from the colony. If at the feeding ground itself there is a super-abundance, there will be no appreciable diminution of the food available to the individual bird.

There is not space here to discuss the assumption, supported by much circumstantial evidence, though not proved by quantitative information, that food is a factor controlling the numbers of many sea-birds. One may, however, cite the data of Jespersen (1930) on the general correlation of seabird and plankton density in the North Atlantic, and the correlation shown by Fisher between the southward spread of the fulmar and its increased food-supply derived from man's activities (published in these Proceedings.) For the guillemots, the availability of food will be most important when the young are on the ledges, and the parents must waste little time in foraging. It will be of little importance, however, after the pelagic dispersal.

Outside the breeding season, it seems that *lomvia* is rather more pelagic than *aalge*, occurring further from the coast (Rankin and Duffey 1948, Arnold 1948). The correlation with food, if any, is unknown.

## General Discussion

Maps of breeding colonies (see esp. Ferdinand 1947 for the Faeroe Islands) show that the guillemot colonies, particularly those in the high arctic, are relatively large and localised, situated usually on oceanic islands and bold promontories. Naturally such situations provide in general the higher and steeper cliffs, most free from predators. However, not all such cliffs are utilised. It seems that an important condition is the proximity of suitable feeding grounds during the breeding season, as emphasised earlier by Eliot Howard (1920). We may contrast *Cepphus grylle*—the black and Mandt's guillemot of the Atlantic, and the pigeon guillemot of the Pacific. These have a more even distribution in scattered groups, nesting often singly (though with a social display); but are, however, inshore-feeding, scattering along the coasts for benthic fish, crustacea and molluscs.

The auk colonies of the high arctic are moreover well integrated and compact; the territories of different birds are taken up, eggs laid and young fledged all within narrow limits of time. Further south it is more usual for the colonies to be split up into subgroups which are integrated within themselves, but not together in the colony as a whole (Perry 1940, Johnson, 1941).

Whatever the mechanism of this closer co-ordination, the adaptive value is clearly in allowing successful breeding within a short arctic summer.

Possibly the descent *en masse* of the young also minimises the effect of predators, which, chiefly in the form of glaucous gulls (*Larus hyperboreus*), are more numerous round the arctic colonies than are predatory gulls further south. We may again contrast Mandt's guillemot (*Cepphus grylle mandtii*) which is a relatively sedentary species even in the high arctic. Here nesting is often solitary, and the young may not fledge until as late as September, when they descend to the sea fully developed.

Considering the zoogeographical picture of breeding distribution, we may ask what factors limit the respective distributions of the two species and prevent further mixing. This is a general problem in zoogeography, and the factors concerned must be climatic. But we do not know whether it is temperature (sea or air temperature) acting directly on metabolism, or whether food-supply, dependent ultimately on hydrographical conditions, that limits the distribution, leaving one species at a selective disadvantage in the range of the other.

That the balance is a fine one is shown by the gradation of replacement in Iceland mentioned above, and by the cline of percentage of bridled birds among the total population of *aalge*. The percentage increases gradually northwards, but *decreases* again northwards in Iceland (Southern and Reeve, 1941). It may be that the presence of *lomvia* here affects the bridled birds more adversely than the typical form; it is difficult to believe in a reversal of the effective climatic factors, whatever they may be.

Our ignorance of the factors that operate in this type of problem leads one to suggest two lines of attack. First, greater co-operation with oceanographical and fishery research work by those studying marine birds, following the great lead of Murphy (1936) and of Jespersen (1930). We are now learning much about the pelagic distribution of various seabirds, but little about the correlation of this distribution with ocean currents, and with the planktonic or nektonic animals that may comprise the food. Indeed we have few quantitative data on food, even with so well-known a species as the fulmar. This may be attributed in part to the small economic importance of seabirds within the sphere of marine research. Secondly, more experimental work; though admittedly land-birds would be more tractable in the laboratory. A parallel case in some ways to the guillemots, and one which should repay experimental analysis, is that of the Hooded and Carrion crows (*Corvus corone*) which, as is well known, do hybridise in their zone of overlap, though the hybrids do not spread. Here it should be possible to compare, for instance, the survival of hybrids and of both parent forms under parallel conditions of temperature and humidity. Thus some beginning could be made in analysing "selective balance" between related species, a zoogeographical and ecological situation where the dynamic factors involved are still largely obscure.[1]

## Summary

1. The ecological relationships existing between the two guillemots *Uria aalge* and *Uria lomvia* at the mixed colonies in the North Atlantic and Pacific have been analysed. It is shown that the two species breed together, separating only at the margins of the colonies, where slightly differing habitat preferences are seen.

Competition appears to exist only in the rare instance of colonies where nesting space is restricted.

2. The food of the two species in any one area is probably the same. Feeding is gregarious, and this habit is shown to be of advantage to a socially-nesting sea-bird species, or group of species.

3. Food is considered to be an important factor limiting the size and distribution of the breeding colonies of these sea-birds.

4. The problem of the *modi operandi* of climatic and ecologic factors upon distribution is briefly discussed, and the need stressed for (a) closer cooperation with oceanographical investigations, and (b) further experimental work on related problems.

*Discussion:*

A. Allen: In a colony of *Uria aalge* on the north shore of the Gulf of St. Lawrence (St. Mary's Refuge. Fog Island), Johnson discovered a single *Uria lomvia* nesting in a colony of *U. aalge* about 1939. It was on a narrow ledge with about 20 *U. aalge* and near the middle of the flock. I visited the colony in 1946 and found what appeared to be the same bird on the same spot but in the meantime there had been no increase in the numbers of *lomvia* in this or adjacent colonies of *aalge* as far as is known.

F. Salomonsen: The suggestion that differences in the temperature of the upper waterlayer are limiting factors is probably correct. The distribution of the various races of alcids in the northern hemisphere corresponds to the temperature differences, just as is the case in the *Tubinares* of the southern hemisphere which ecologically replace the alcids of the northern hemisphere.

[1] Since the above was written, the work of Udvardy (published elsewhere in these Proceedings) has come to the writer's attention.

R. H. Pough: Have you had a chance to compare the stomach contents of a series of specimens of each species collected at the same period in the same colony? It might reveal a selection of food organisms within the same breeding area.

D. E. Sergeant: Only a few stomachs of adults and young of both species were collected at Bear Island and examined. The results are inadequate to reveal whether such a selection occurs.

## References

Arnold, L. W., 1948. Observations on Populations of North Pacific Birds. Auk *65*, 553-8.

Bent, A. C., 1919. Life Histories of American Diving Birds. Bull. U. S. Nat. Mus. *107*, 1–245.

Cottam, C., 1936. Food of Arctic Birds and Mammals . . . J. Washington Acad. Sci. *26* (4), 165–177.

Ferdinand, L., 1947. Studies of the Bird Life of the Faeroes. Dansk. Ornith. For. Tidsskr. *41*, 1.

Foster, R. J., Baxter, R. L. and Ball, P. A. J., 1951. A Visit to Grimsey (Iceland) July–August 1949. Ibis *93*, 53–62.

Gabrielson, I. M., 1944. Some Alaskan Notes. Auk *61*, 270–287.

Gorbunov, L., 1925. The Loomeries of Novaya Zemlya. Trans. (Trudy) Inst. Expl. North *26*, 1–47.

Hachisuka, M., 'Birds of Iceland.' London 1927.

Hartley, P. H. T. and Fisher, J., 1936. The Marine Food of Birds in an Inland Fjord Region in West Spitsbergen. Journ. Anim. Ecol. *5*, 370–389.

Howard, Eliot, 'Territory in Bird Life'. London, 1920.

Jespersen, P., 1930. Ornithological Observations in the North Atlantic Ocean. Oceanogr. Rep. Danish "Dana" Exped., 1920–22.

Johnson, R. A., 1938. Status of the White-eyed Murre. Auk *55*, 56–61.

—— Nesting Behaviour of the Atlantic Murre. Auk *58*, 153–158.

Krassovski, S. K., 1937. Studies on the Biology of *Uria lomvia*. Trans. Arctic Inst. Leningrad *77*, 33–91.

Murphy, R. C., 1936, Oceanic Birds of South America, Vol. I, pp. 59–110. New York.

Palmer, W., 1899. The Avifauna of the Pribilov Islands. In: D. S. Jordan: The Fur Seals and Fur-seal Islands of the North Pacific Ocean, Vol. III, p. 355. Washington.

Perry, R., Lundy, Isle of Puffins, London 1940.

Rankin, M. N. and Duffey, E. A. G., 1948. A Study of the Bird Life of the North Atlantic. Brit. Birds, supplementary No., Vol. *41*, July 1948, pp. 1–42.

Roberts, B. B., 1934. The Gannet Colonies of Iceland. Brit. Birds *28*, 100–5.

Salomonsen, F., 1944. The Atlantic Alcidae. Göteb. Vet. o. Vitt.-Samh. Handl. Ser. B, *3*, (5).

Southern, H. N. and Reeve, E. C. R., 1941. Quantitative Studies in the Geographical Variation of Birds—the Common Guillemot (*Uria aalge*). Proc. Zool. Soc., Lond. A, *111*, 255–276.

Steinbeck, J. and Ricketts, F. F., Sea of Cortez, New York 1941.

Stejneger, L., 1885. Results of Ornithological Explorations in the Commander Islands and Kamschatka. Bull. U. S. Nat. Mus. *29*, pp. 382.

Witherby et al., A Handbook of British Birds, Vol. V, London, 1941.

Yamashina, Y., 1931. Die Vogel der Kurilen. J. Orn., Leipzig *79*, 491–541.

# The Food of the North-European Gulls.

*R. Spärck.*

*Zoological Museum, Copenhagen*

There has been much discussion of the problem whether our North-European gulls do any damage of importance to other bird life, to fishery and agriculture. This discussion is still going on as we learned a few days ago at the Conference of the International Committee of Bird Preservation. Everybody who has anything to do with bird reserves is often faced with this problem, and this is the reason why some years ago I started an investigation regarding the food of the Danish Gulls by means of an analysis of the stomach contents. There are only few and scattered records in the literature on this subject. Collinge, Otterlind, Bergman and others have made analyses of the stomach contents of some gulls, but the material is small, only some few hundred stomachs have been analysed as yet. The results of this investigation will be published in the Danish Review of Game Biology, vol. 2. I shall not waste space by going into detail but only give the main lines and results.

The material principally belongs to the three species, which are common breeders in Denmark:

| | | | |
|---|---|---|---|
| Black-headed Gull (*Larus ridibundus*) | about | 3 500 | stomachs |
| Common Gull (*Larus canus*) | » | 3 000 | » |
| Herring Gull (*Larus argentatus*) | » | 1 000 | » |

besides these a smaller number of the Greater Black-backed Gull (*Larus marinus*), the Lesser Black-backed Gull (*Larus fuscus*) and the Kittiwake (*Rissa tridactyla*) have been examined.

Fig. 1 shows how the different items expressed in percentage have been found in the 3 500 specimens of Black-headed gulls examined. It is evident that insects, which have been found in 55 % of all specimens examined represent the main source of food. The second important item of food is offal and earthworms. Fish and crustaceans have only been found in 15 % of the stomachs and in almost the same percentage remains of plants have

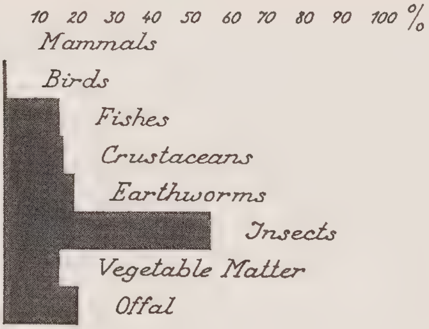


Fig. 1. The distribution of the items of food in the Black-headed Gull.

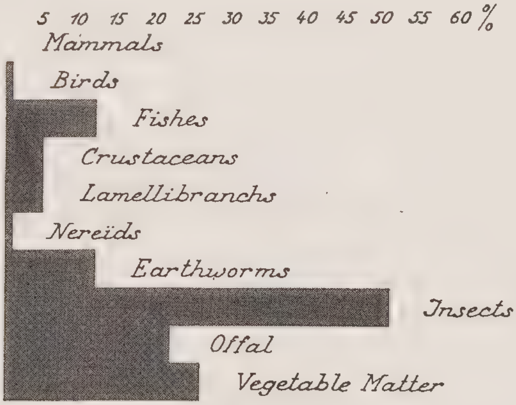


Fig. 2. The distribution of the items of food in the Common Gull.

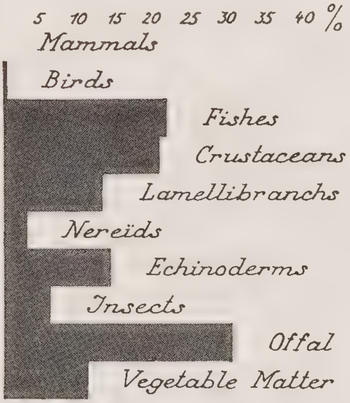


Fig. 3. The distribution of the items of food in the Herring Gull.

been found. Fig. 2 shows in the same way the distribution of the items of food in the Common Gull. The picture is the same: insects are the principal food, fish, crustaceans, lamellibranchs, polychaetes and other marine species are of less importance. The only difference between these two species of gulls is that plants and offal seem to play a slightly greater rôle in the Common Gull than in the Black-headed Gull. Fig. 3 shows, in the same way, the food of the Herring Gull. The picture here is quite different. Insects are of very little importance, only 10 %, while fish, crustaceans, echinoderms and lamellibranchs occur in 15–20 % of the specimens examined. Offal is very important as an item of food for the Herring Gull, since it has been found in 35 % of the gulls examined. Also in this gull, vegetable matter amounts to 10 %.

Thus the main result, as regards their food habits, is that although the gulls may be considered as omnivorous, there seem to be distinct differences between the species investigated.

Two of the species, *Larus marinus* and *Rissa tridactyla,* are shore birds, feeding on fish and marine invertebrates. *Larus argentatus* is a shore bird too, but more associated with civilization, offal playing a great part in its diet, and this may explain the terrific increase in this species during the last decades. *Larus fuscus* is partly an insect feeder, partly a fish eater, this being in good agreement with the ecology of this species, breeding on the shore, but migrating in many cases through the Continent. *Larus canus* and *Larus ridibundus* are not marine or shore birds in their food habits but land birds relying on a diet consisting of insects, earthworms, plants etc.

The damage done by the gulls as a whole is of very little significance. A species, such as the Kittiwake, feeding mostly on zooplankton and small pelagic fishes can do no damage at all. The Greater Black-backed Gull and the Herring Gull may, to a certain degree, be injurious to fishery, but, on the other hand, the Herring Gulls eat quantities of crabs which are noxious animals to fishery, and they may further be beneficial in eating quantities of offal. It must be admitted from the point of view of other bird life that these larger gulls eat the eggs and young of other bird species, although remnants of birds have only been found in less than 2 % of the Herring Gulls examined. This damage seems to be local, in several Danish bird sanctuaries where the number of breeding Herring Gulls has increased in the last few years, the number of other breeding birds has also increased during the same period. As regards the Lesser Black-backed Gull the damage done to fishery is counterbalanced by the benefit to agriculture caused by its insect diet. The Common Gull and the Black-headed Gull are of no importance to fishery apart from ponds where in rare cases some damage may be done. From the point of view of agriculture these two small species are decidedly useful; they may also be regarded as useful to other bird life, since other birds (wildfowl etc.) often prefer to breed in the colonies of gulls. Considering the North-European gulls as a whole they are, from the point of view of fishery, only slightly injurious and only the larger species do any damage; from the point of view of agriculture they are beneficial and from the point of view of other bird life the larger species are in some cases locally injurious, the smaller species useful.

*Discussion:*

L. de Beaufort: Is it not curious that *Larus argentatus* and *L. fuscus*, which are systematically nearly related, take such different food?

R. Spärck: Even if *Larus argentatus* and *L. fuscus* are very nearly related systematically, they are very different in their ecology. *L. fuscus* migrates through the continent, whereas *L. argentatus* is a shore-bird throughout the year.

D. Sergeant: I would like to mention the change of food habits in some of these gulls that has occurred of recent years. (It is well known that *Larus ridibundus* has become a scavenger in towns and a follower of the plough). In Great Britain, *Larus marinus* has become a common scavenger, even in summer, at fishing ports. In one area of East Anglia, it now winters inland and feeds in heathland, apparently upon carrion such as dead rabbits (*Oryctolagus cuniculus*). In my opinion the increase of these gulls, that has occurred in the last fifty or so years in Britain, may be attributed largely to their utilization of new foods.

R. Spärck: As regards *Larus argentatus* and also *L. canus* and *L. ridibundus* an alteration in the food-ecology seems to have been observed in Denmark.

S. Hörstadius: These interesting investigations cannot give a real picture of the damage done by gulls as there will be hardly any remnants left of unbrooded eggs or of eggs brooded only a few days. Moreover, in Sweden *Larus marinus*, which was not treated in detail in the paper, is a particularly great robber of eggs and young birds.

R. Spärck: It is true, that the presence of eggs cannot be shown by analysis of stomach contents. *L. marinus* breeds very rarely in Denmark.

# Difficulties in stomach analysis

*E. van Koersveld*

*Phytophathological Service, Wageningen, Netherlands*

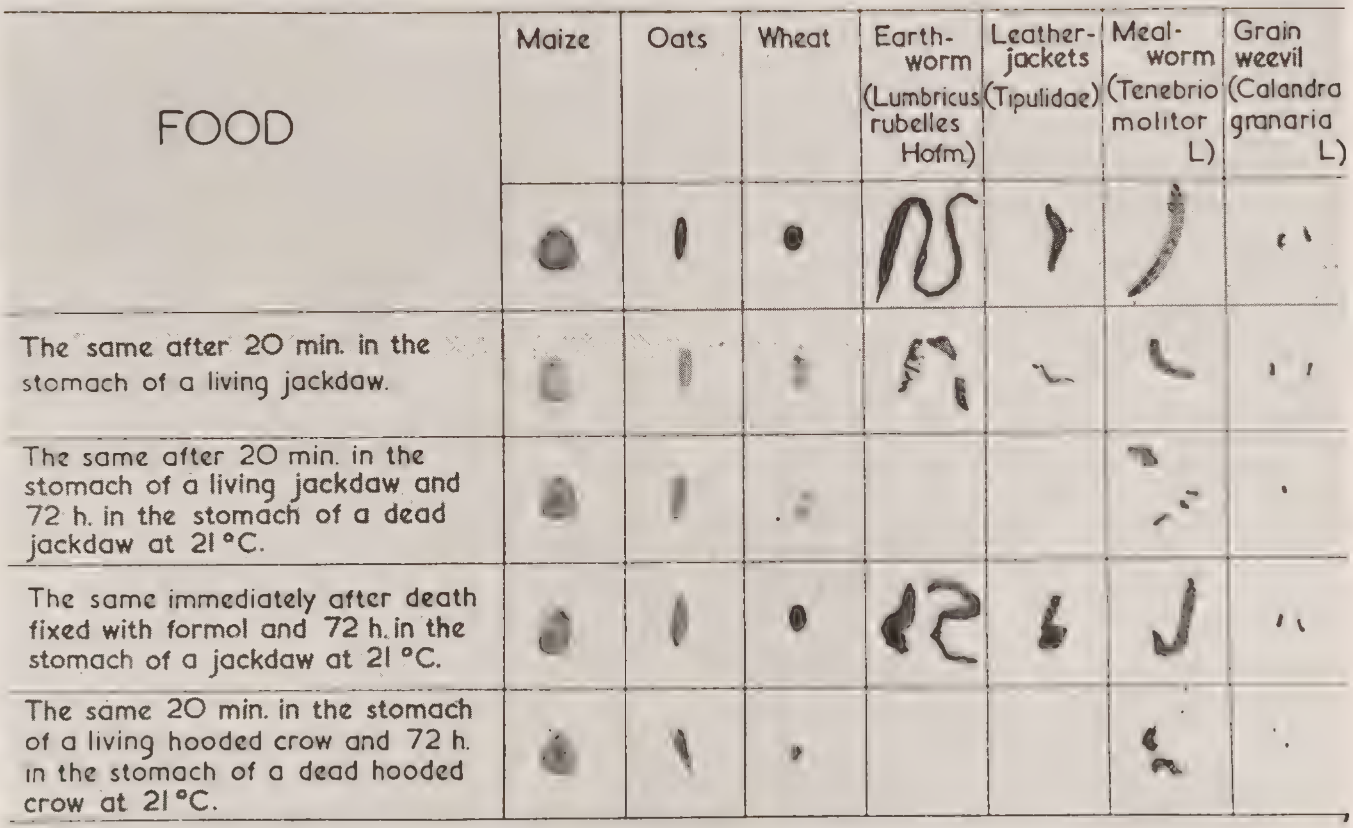
My predecessor Dr. H. N. Kluyver investigated the stomach contents of 50 jackdaws (*Corvus monedula spermologus* (Vieill.)), which were collected during the winter. Following up these researches I investigated the stomach contents of 50 jackdaws collected during the summer. To my surprise I found in many stomachs a pulpy mass; consequently only very few insects could be identified as to the species. The difference between summer and winter stomachs can only be explained by accepting that digestion of the stomach contents continues after death. The digestion will proceed, dependent on the temperature and the time which lies between the killing of the bird and the investigation of the stomach.

To prove this point some jackdaws were fed with a grain of maize, a grain of oats, a grain of wheat, an earthworm (*Lumbricus rubelles* Hofm.), a leather jacket (*Tipula*-larva), a mealworm (*Tenebrio molitor* L.-larva) and 2 grain weevils (*Calandra granaria* L.)

One jackdaw was killed 20 minutes after taking the food. The stomach was immediately dissected. We found that digestion, especially of the softer animals like the earthworm and the leather jacket, was already far advanced.

A second jackdaw was also killed 20 minutes after taking the food but was then kept for 3 days (about the maximum time which a postal parcel takes in the Netherlands) in a thermostat at 21° C, a regularly occurring summer temperature in the Netherlands. It appeared that the earthworm and the leather jacket had completely vanished; we found only the remains of the mealworm and grain weevils; the grain of wheat was strongly affected; the grain of oats much less affected; and the grain of maize was unaffected.

A third jackdaw was killed immediately after taking the food, and then a few cc of 10 % formalin were poured into the alimentary canal. This



| FOOD | Maize | Oats | Wheat | Earth-worm (Lumbricus rubelles Hofm.) | Leather-jackets (Tipulidae) | Meal-worm (Tenebrio molitor L) | Grain weevil (Calandra granaria L) |
|---|---|---|---|---|---|---|---|
| | | | | | | | |
| The same after 20 min. in the stomach of a living jackdaw. | | | | | | | |
| The same after 20 min. in the stomach of a living jackdaw and 72 h. in the stomach of a dead jackdaw at 21 °C. | | | | | | | |
| The same immediately after death fixed with formol and 72 h. in the stomach of a jackdaw at 21 °C. | | | | | | | |
| The same 20 min. in the stomach of a living hooded crow and 72 h. in the stomach of a dead hooded crow at 21 °C. | | | | | | | |

Fig. 1. Explanation in text.

bird was kept for 3 days at 21° C. It proved that the stomach contents were almost unaffected.

Finally a hooded crow (*Corvus cornix cornix* L.) was forced to take the same food. The bird was killed after 20 minutes and then kept at 21° C for 3 days. It proved that the stomach contents were still more affected than in the case of the jackdaw, which was treated in the same way; only a few remains of the mealworm and the grain weevils, which could not be identified, were found; the earthworm and the leather jacket had completely disappeared. The grain of wheat was very strongly affected, the grain of oats strongly and the grain of maize much less affected.

We consequently arrive at the conclusion that the digestive effect of the gastric juices and the autolysis of the foodparts continue after the bird's death. In particular, animal remains are affected. Thus a wrong interpretation of the food which is taken by the bird may be the result. This can be prevented by dissecting the stomach of the bird immediately after killing and fixing the contents. In case the birds are collected in different parts of the country, it is necessary to equip the collectors with a bottle of 10 % formalin to fix the stomach contents.

# Heat Resistance in Birds

*M. D. F. v. Udvardy*

*Zoological Institute, Uppsala*

The effect of warm climate as a distribution-limiting factor is especially emphasized by Twomey (1936). In his opinion, the imported European birds in the United States became distributed only in regions, which correspond to their original breeding localities in Europe, as regards temperature and precipitation. According to Twomey, the suitability of the climate is most important during the breeding period, but he also refers to American birds which have similar climatic restrictions in the breeding period, as well as in the wintering places.

Ekman (1909), and later on Merikallio (1917) investigated some Arctic species of Northern Scandinavia, which also have breeding stations on the Baltic coasts. These points of the coast have as low a mean-maximum temperature in the summer months as that of Northern Lapland, their greater breeding area. This applies especially to *Clangula hyemalis* and *Plectrophenax nivalis*. Therefore, it seems that the survival of their stock is correlated with the maximum temperature during the breeding period.

It has been found possible to draw the same conclusion as regards *Numenius arquatus, Turdus pilaris* and *Carduelis spinus,* as well as *Anthus pratensis* and *Circus pygargus,* all of which are breeding birds in NW Hungary since the end of the nineteenth century. Being abroad, I was unable to compare the mean-maximum temperature data. However, the mean temperature of the summer months decreased in Hungary during the same period. Thus, the mean temperature of May between 1870–1940 was 1.18° C lower than that between 1800–1870. The type of landscape in NW Hungary does not differ greatly from that of the breeding places in the northern parts of Central Europe, and this circumstance facilitated the expansion of the species in question when the drop in summer temperature made it possible (Keve and Udvardy, 1950).

In addition to the very conspicuous macroclimatic effects mentioned above,

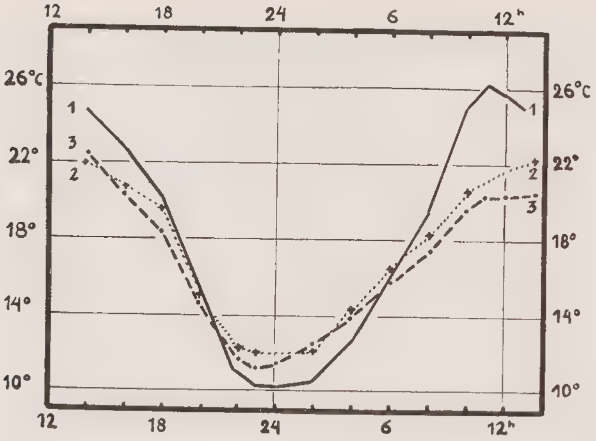


Fig. 1. The microclimate in deserted nests of *Sylvia communis* (1), *S. curruca* (2), and *S. borin* (3). Tvärminne, July 26–27, 1948.

the differences in the microclimate are also very important in connection with the nesting behavior of birds. In order to illustrate the differences in the microclimate even with congeneric species having the same major habitat, I measured the temperature in nests of three *Sylvia* species in Southern Finland during the warmest days of the summer of 1948. The most extreme microclimate prevailed in the Whitethroat nests, which were situated in turf in open places or in bushes. This bird sings regularly in open places, e.g., on the tops of trees or bushes, and often forages in grassy vegetation or cereal crops. The nests of the Lesser Whitethroat and Garden Warbler possessed a more temperate microclimate, but these species mostly live in the shade and the nests are located in the interior of coniferous bushes (Fig. 1).

The organism of a bird is very sensitive to fluctuations in the temperature of the external environment. Giaja and Gelineo (1936) found that the body temperature of the bird adjusts itself to variations in the outside temperature. My overheating experiments on domestic pigeons demonstrate that there is no homoiothermy at outside temperatures above 33° C, and that the body temperature curve runs parallel to that of the outside temperature (Fig. 2).

As is known, there are two kinds of thermoregulatory systems in the organism, which act to prevent overheating. Physical thermoregulation implies increasing loss of temperature by evaporation (rising respiration, panting). The diminishing of the rate of basal metabolism, resulting in a di-

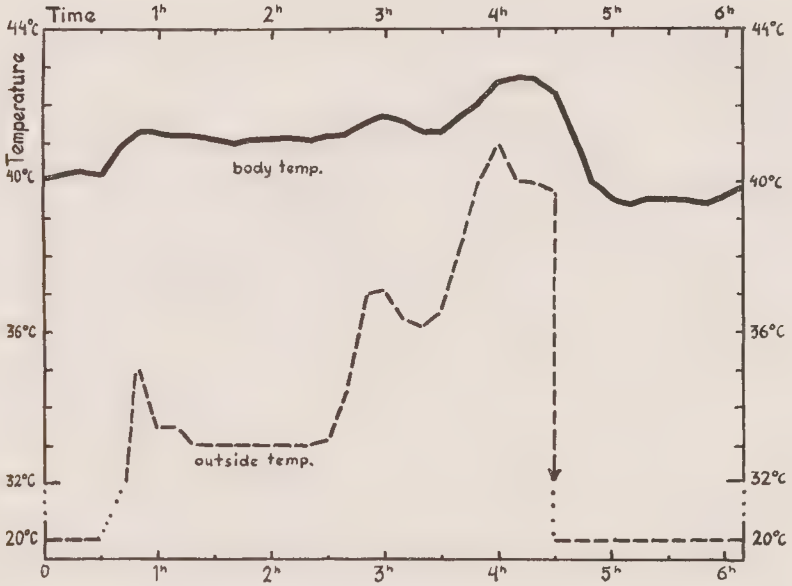


Fig. 2. Body temperature curve of domestic pigeon, adapted to 20° C outside temperature, with varying outside temperatures.

minishing of heat production is called chemical thermoregulation. Recently Mansfeld (1949) showed that the thyroid gland in mammals secretes hormones, which are able to neutralise thyroxin and thus cool down the organism. Accordingly, the thermal adaptation of birds found by Giaja and Gelineo (l.c.) would mean that the bird adjusts the level of its basal metabolism with the aid of hormones, so that its organism is in harmony with the outside temperature. In my opinion, there is a sign of hormonal heat regulation, namely that the body temperature drops below the normal temperature even after a heating period of one hour. This is demonstrated by experiments with *Parus atricapillus, Carduelis linaria, Aegolius funereus,* etc. (Fig. 3).

Equally adapted specimens of different species show different degrees of heat resistence. 3 *Parus cristatus* and 2 *Parus atricapillus,* all adapted to 23° C and adjusted to 33° C outside temperature, were kept under identical experimental conditions, their body temperature being registered with the aid of a thermocouple. Within 30–40 minutes the body temperature of the Crested Tits rose from a normal temperature of 40–41° C to above 45° C, when the birds died. The body temperature of the Willow Tits rose in one hour to 42° C and 44.2° C respectively, but the birds were not affected.

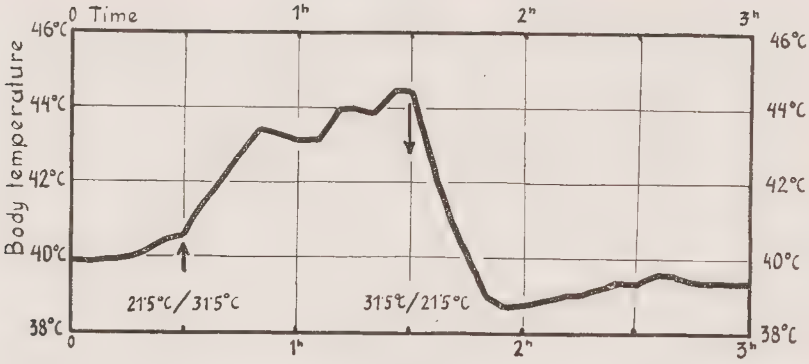


Fig. 3. Body temperature curve of *Carduelis linaria* with the outside temperatures indicated.

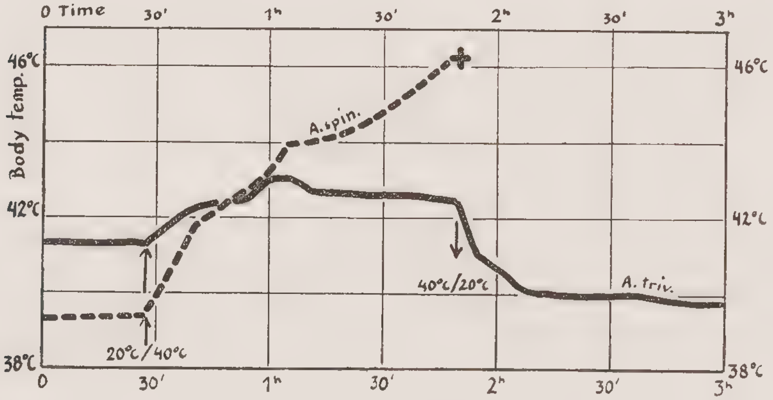


Fig. 4. Body temperature curve of *Anthus trivialis*, and *A. spinoletta littoralis* Brehm, with the outside temperatures indicated.

Two other examples are the Rock Pipit (*Anthus spinoletta*) and the Tree Pipit (*Anthus trivialis*). The Rock Pipits rapidly died at 40° C outside temperature, while the Tree Pipits were not affected (Fig. 4).

A series of similar experiments on different species seems to support the results of Kendeigh's (1945) starvation experiments, which indicated that the heat resistance of the northern species is less than in the southern species of the American birds investigated. On the other hand, birds of open habitats, i.e., birds of more extreme microclimates, show better thermo-regulation against heat than bird of more temperated habitats, viz., forests.

## References

Ekman, S., 1909. Ymer 2: 261.
Giaja, J. & S. Gelineo, 1936. C. R. Soc. Biol. Paris, 122: 343.
Kendeigh, S. C., 1945. Journ. Wildlife Manag. 9: 217.
Keve, A. & M. D. F. v. Udvardy, 1950. Proc. X. Int. Ornith. Congr. (in the press).
Mansfeld, G., 1949. The Thyroid Hormones, pp. xii + 157. Muller, London.
Merikallio, E., 1917. Fauna o. Flora 12: 72.
Twomey, A. C., 1936. Ecology 17: 122.

# Birds of the North Atlantic

*E. M. Nicholson*

*London*

Recent observations have given us a rough preliminary picture of the broad distribution of the main species of birds which inhabit the North Atlantic during part or all of the year. These observations, stimulated by the work of Jespersen, Murphy, Alexander, Wynne-Edwards, Rankin and Duffey and others, have shown that different parts of the ocean each have their characteristic summer, winter and passage birds, according to their latitude and longitude, their distance from land, the depth of water and its richness in plankton and fish, and other factors. In fact, large regions of the ocean can be distinguished within which the bird population shows as wellmarked and understandable differences from other regions as that of Sweden does from that of Great Britain. In order that these differences can be recognised and studied it is becoming essential that agreement should be reached upon defined regions and subdivisions of the ocean, to provide a framework serving the same purposes as the boundaries of countries and provinces on land. Mere points on the map defined by latitude and longitude do not form a convenient framework, any more than names of villages do on land. Nor, so far as I have been able to trace, has any system of regions been proposed, for other purposes, which fully meets the need.

I have therefore prepared, and published in Bulletin No. 36 of the British Trust for Ornithology in January 1950, a proposed series of Regions of the North Atlantic, which Miss J. H. Lidderdale has kindly mapped on the basis of Mollweide's Projection, and which is here exhibited. It covers the area from the Equator up to 80 Degrees North. Each region is 10 degrees of longitude in breadth and 10 degrees of latitude in depth, which at the latitude of southern Britain gives areas about the size of France and Great Britain combined. Each region is allotted a name chosen to indicate as clearly as possible in which part of the ocean it lies, without duplicating geographical terms having other accepted meanings, but without unneces-

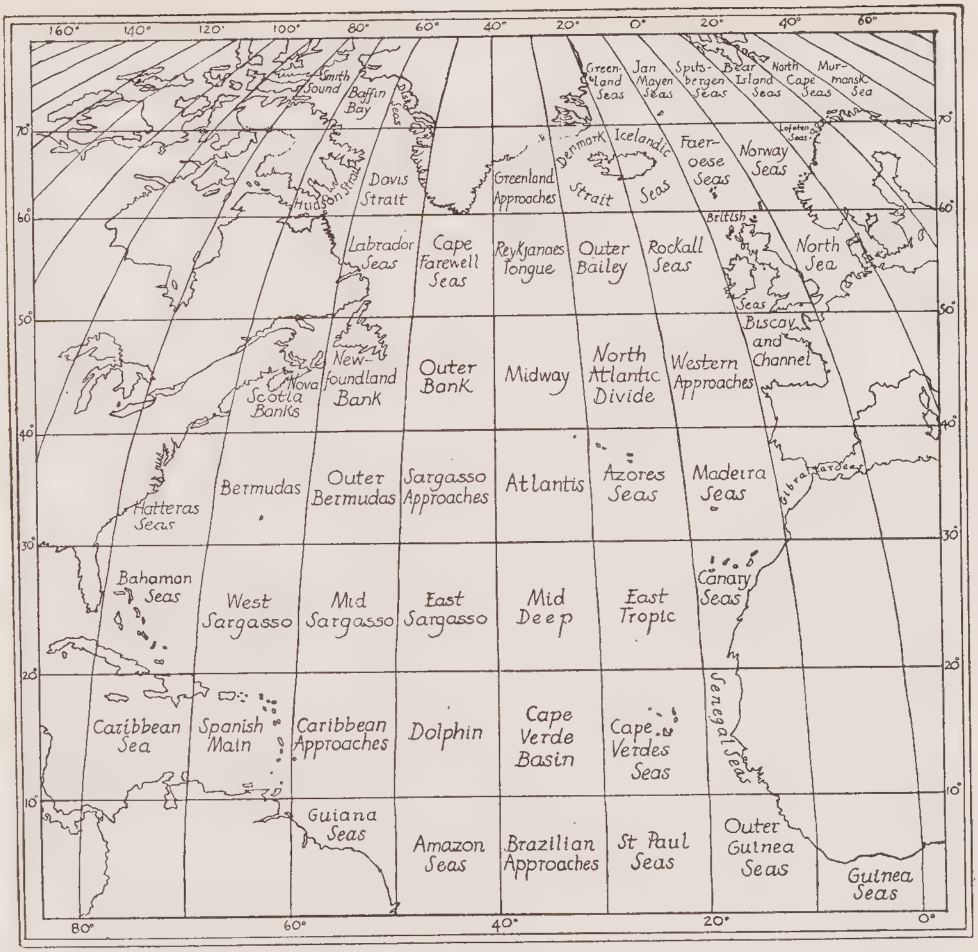


Fig. 1. A proposed series of Regions of the North Atlantic.

sarily proposing new names. The regions should be understood to consist of tidal waters outside territorial limits only, and where any land falls within the limits of one of the regions it should be understood to be excluded, together with its territorial waters, and should continue to be described as at present. In other words the proposed Regions are designed to fill a gap, not to supersede or complicate any existing geographical descriptions for land areas and their territorial waters. Also, wholly landlocked seas such as the Baltic and Mediterranean, and certain odd fragments of sea in or near coastal waters have been omitted.

For more precise purposes each of the ten-degree quadrilaterals named as Regions can readily be subdivided into a hundred degree-quadrilaterals or Provinces, each being one degree of longitude broad and one degree of latitude deep. For reference these Provinces can conveniently be cited by stating, after the name of the Region in which they lie, the number of the latitude parallel forming the base and the number of the longitude meridian forming the west side, inserting a 0 in front of figures below 10. Thus for example St Kilda lies in British Seas 57.09. By this system anyone having any ordinary accurate map or chart of the North Atlantic together with the diagram or a list of the 59 named Regions can refer to bird distribution in any one of some hundreds of precisely defined areas comparable with the subdivisions universally used for land areas, and equally serviceable. Where exact points need to be recorded degrees and minutes can of course still be used in the normal way, and each of these positions can readily be placed in its correct Region and Province without having to consult a gazeteer, as would often be the case on land.

To conclude with some brief illustration, the shipping route from the English Channel to New York runs across the seven Regions, Biscay and Channel, Western Approaches, North Atlantic Divide, Midway, Outer Bank, Newfoundland Bank and Nova Scotia Banks. In Western Approaches (10–20 deg. W., 40–50 deg. N.) the sea is mostly deeper than 3 000 metres, stormy but mild and the Kittiwake (*Rissa tridactyla*) is the commonest winter bird, but is absent in summer. The Gannet (*Sula bassana*), Little auk (*Alle alle*) and other species also winter. Cory's Shearwater (*Puffinus kuhlii*) is frequent from March to September but then withdraws south and west. Skuas (*Stercorarius sp.*) and land-birds migrate across this Region. By contrast in Outer Bank (40–50 deg. W. and 40–50 deg. N.) icebergs and fog are common and the depth in parts is under 200 metres. Here Kittiwakes and Brunnich's guillemots (*Uria lomvia*) appear common from January to May, Leach's petrels (*Oeanodroma leucorrhoa*) from April to October, Little Auks from March to May and Cory's Shearwaters in September-October only, while Great Shearwaters (*Puffinus gravis*) are common in May-June. So each Region, once recognised, proves to have its characteristic bird life.

*Discussion*:

R. C. Murphy considered the naming of the ten-degree squares practical, and the designations appropriate. Possibly one or more of the areas might receive names of even better geographical or historical significance, which might make them even simpler to recall.

# Sea Birds of the Persian Gulf

*Bernt Løppenthin*

*Copenhagen*

During the two winters 1936–37 and 1937–38 fishery investigations under the direction of the Imperial Government of Iran were carried out in the Persian Gulf. The leader of the expeditions was the Director of the Danish Biological Station Dr. phil. H. Blegvad, who was assisted by three Danish fishermen, the crew of a North Sea motor fishing boat of 34 tons, which had been bought in Denmark and sent to the Gulf in 1936; I was scientific assistant the second winter. The chief aims of the expeditions were practical, to study fish and fishery in Persian waters, to give advice as to the rationalizing of the fishery and to point out edible fishes especially suitable for canning and other industrial purposes. Most of the time, of course, I was occupied by this work, but I was often able to make ornithological excursions, especially around Bushire, our headquarters during our stay at the Gulf, and now and then we paid flying visits to various islands, both inhabited (Larak, Hormuz, Henjam, Farur) and uninhabited (Nabiyu Farur, Nabiyu Tunb, Shatwar, Farsi, Arabi, Harkus). I am very much indebted to Dr. Blegvad for his interest in my spare time work.

I left Denmark on November 15, 1937, and went via Trieste—Haifa—Damascus—Baghdad to Teheran; after some time there we went by car to Khorram Shahr, where the boat was lying, and after a couple of days we started. On the evening of December 17 we passed from the mouth of Shatt-al-Arab into the Persian Gulf. During the next two months we fished in the waters near Bushire from the island of Kharg in the North to the villages of Daiyir and Kangun (abt. 28° lat. N. 52° long. E.). During the latter half of February we had a rather tedious stay at Bandar Shahpur for repairing the ship in a floating dock and continuous bad weather prevented me from doing much ornithological work. From the beginning of March we again worked in the neighbourhood of Bushire, and on March 14 we left the place, paid a short visit to Bahrein and went eastwards to the Strait of Hormuz and the Gulf of Oman. The most remote point we reached was Chahbar (abt. 25° lat. N. 60° 30′ long. E.). On April 14 we were back at Bushire, and after ten days there Dr. Blegvad left for Teheran, while I went with the fishermen to the islands of Farsi, Arabi and Harkus (abt. 28° lat. N. 50° long. E.). We needed a fishery station in that part of the Gulf. I shall not deny, however, that my personal interest rather lay in a breeding place of the Sokotra Cormorant, which I hoped to find there, and actually found. On April 28 we entered Shatt-al Arab in the evening reaching Khorram Shahr, where the boat was laid up. I spent by far the most time on the coast or at sea. On this account only coastal and true marine birds will be dealt with in this paper.

When an ornithologist travels in the Strait of Hormuz and the Gulf of Oman great attention will always be paid to the occurrence of *Puffinus persicus* Hume. I am sorry to say that I stayed in this district from March 22 to April 8 without getting any definite observations on this species. Possibly I saw a flock off Chahbar on March 31 but in the far distance. Ticehurst (1926 p. 6) mentions observations from February, March and May, and Cheesman (ib. p. 7) saw "several flocks . . . 22–30 in each" as far West as abt. 26° lat. N. 55° long. E. (between the islets of Nabiyu Farur and Abu Musa). According to a statement made by Sir Norman Kinnear the breeding place of this species is on the Maldives or the Laccadives.

After this rather problematic matter, I shall give a list of species of seabirds observed or collected by me between December 17, 1937, and April 28, 1938. I shall begin with the breeding species which are more or less resident and afterwards mention the winter-visitors and passage-migrants.

*Pelecanus onocrotalus* L. was fairly common in the inner parts of the Gulf, especially around Bandar Shahpur. Probably a breeding place is somewhere in the neighbourhood of this settlement, from where (Khor Musa) Oates (1902 p. 217) mentions some eggs. I did not see Pelicans south of Bushire.

*Pelecanus crispus* Bruch was seen once only just north of Bandar Shahpur on February 22, not in the Gulf proper. Oates (1902 p. 217) mentions eggs from the Persian Gulf.

*Phalacrocorax nigrogularis* Ogilvie-Grant & Forbes, the Sokotra Cormorant, was next to the Persian Shearwater the species of bird, which I was most anxious to come across. This species was first known from Sokotra in December, 1898 (Ogilvie-Grant & Forbes 1899, p. 3, and id. 1903, p. 49), but no breeding place was found in this district. Obviously the Sokotra Cormorant only breeds in the Persian Gulf. The first time a breeding place was visited was certainly on June 11, 1905, when Sir Percey Cox went ashore on the two islets of Um-al-Maradim and Qaru off the coast of

Kuwait, but on this occasion only dried-up corpses of young and half-grown Cormorants were found; no species is mentioned (Ticehurst 1926, p. 733), but certainly they cannot have been anything but Sokotra Cormorants. The best known breeding place is on the island of Halul, where eggs and young have been found on January 21, 1919, and March 19, 1921; on the latter date Cheesman found many young on the wing, and he roughly estimated a flock of 10 000 birds; at the end of April, 1920, no Sokotra Cormorants were seen at Halul (Ticehurst 1926, p. 731–32). From the end of December, 1937, till we left the Gulf I saw Sokotra Cormorants in different localities of the Persian Gulf and the Strait of Hormuz, i.e. Bushire, Bahrein, Sheikh Shuaib and Shatwar, Larak, Bandar Abbas and last but not least at the islets of Farsi, Arabi and Harkus. From "The Persian Gulf Pilot" I had learned that Arabi sometimes was nearly covered with eggs, especially of Cormorants, and Ticehurst (1926, pl. III) shows a photograph of young Sokotra Cormorants said to have been taken on Farsi. Early in the morning of April 25 I went ashore on Farsi; 10–12 adult and immature Sokotra Cormorants were seen on the island, but no breeding place was found. Afterwards we steered towards Arabi about fifteen miles farther south. When we approached this islet the beach appeared to be covered with black boulders, which suddenly began to run about and shortly after took to their wings. About 2 000 Sokotra Cormorants were seen at Arabi, and about 250 nests were crowded in a space of 1 000–1 500 sq. m. with no vegetation. Fifteen nests contained two eggs, the rest only one, all quite fresh. I did not see a single clutch of three, as reported by Cheesman from Halul (Ticehurst l. c.). The birds of Arabi had certainly just begun to lay. The nests were only small heaps of gravel in some places nearly touching each other. Many mummified corpses of young from a previous breeding season were seen in this locality. The Cormorants were flying about as long as we stayed at the island. About a dozen white-bellied young birds were present but no older, immature ones with grey plumage like a bird illustrated by Ogilvie-Grant & Forbes (1903, pl. VI). I had observed birds like this elsewhere in the Gulf, and one was obtained at the island of Shatwar (abt. 27° lat. N. 53° 30′ long. E.) on April 9. Concerning the photograph shown by Ticehurst (1926, pl. III), mentioned above, I am afraid that the photographer (Hindman) has confused Farsi and Arabi; the locality very much resembles that part of Arabi where I found the colony of cormorants. When we approached Harkus on the morning of April 26 a few Sokotra Cormorants went away from the shore, but no nests were found on this island. From the dates mentioned above, it may be supposed that the breeding time of this species is fairly irregular.

*Phaëton aethereus indicus* Hume was seen in the Strait of Hormuz on March 28 and April 7, only one specimen on each occasion; this latter bird was observed south of the island of Tunb. Knowing that nests of this species had been found on Nabiyu Tunb on April 9, 1921, and April 23, 1923 (Ticehurst 1926, p. 730), we landed on this island on April 7, 1938, but we did not observe any living Tropic Birds or occupied nests on that day. We found, however, a small heap of skulls, apparently from birds killed by men some time before.

*Ardea c. cinerea* L. was common along the Persian coast during the whole winter. I do not know whether these birds were stragglers from Shatt-al-Arab and its tributaries or winter-visitors from northern places.

*Ardea p. purpurea* L. was only observed once, at Bandar Shahpur on February 16.

*Demiegretta sacra asha* (Sykes) was fairly common throughout the district. Blue specimens seemed to be slightly more numerous than white ones. The breeding time is April and May. I did not come across any breeding localities.

*Butorides striatus* probably *javanicus* (Horsf.) is mentioned here although the breeding of this species at the Persian Gulf is not sufficiently proved. I saw three specimens on the island of Shatwar on April 9 and obtained two of them, ♂ and ♀; the testes of the former were enlarged, but the ovary of the latter had no enlarged egg-cells. According to Stuart Baker (vol. IV, 1935, p. 474) the normal breeding season in India is end of June to September.

*Platalea leucorodia* L. (subsp.?) was only seen once, at Bandar Shahpur on March 1.

*Phoenicopterus ruber roseus* Pall. was observed now and then in flocks of 50 to 60. I did not see any breeding place.

*Pandion h. haliaetus* (L.) was common throughout the district. A number of nests were seen, mostly on hills on the uninhabited islands. Nabiyu Farur and Nabiyu Tunb had three nests each, all of them empty except one. The inhabited nest was seen in the former of the two islands; it was built on the bare ground. On March 22 it contained two young of five to six weeks.

*Dromas ardeola* Paykull was only seen around Bushire. I observed almost daily from January 13 to February 5 a flock of about 300 birds there. No breeding place was found.

*Charadrius a. alexandrinus* L. was common in most places. I saw injury feigning from March 25, but I did not find the nests.

*Larus hemprichii* Bruch was fairly common in the outer part of the Persian Gulf and in the Strait of Hormuz. I did not see any west of 53° long. E. Breeding does not start till June.

*Larus genei* Brème was fairly common throughout the district. It seems to breed a little earlier than the previous species but not very much before May. I did not see any signs of breeding.

*Gelochelidon n. nilotica* Gm. was common around Bushire and Bandar Shahpur; a single bird was seen at Bandar Abbas on April 5. The Gull-billed Terns greatly preyed on Mud-skippers (*Periophthalmus* and *Scartelaos*) and small Crustaceans in the tidal zone, but I also saw them catch insects over land. The breeding had begun when we left. On April 22 I saw two small colonies on a flat island at Bushire; only three single eggs were seen, but children's footprints indicated that eggs had been collected for food.

*Hydroprogne tschegrava* (Lep.) was fairly common around Bushire and Bandar Shahpur. Breeding had not begun when we left.

*Sterna bergii bakeri* Mathews and *Sterna b. bengalensis* Lesson were very common from the island of Kharg outwards. Breeding scarcely starts till the end of May or later.

*Sterna repressa* Hart. was fairly common in the Persian Gulf. The breeding time is June—July.

*Sterna anaetheta fuligula* Licht. is said to be fairly common. I observed this species now and then but much less often than, for example, the two Crested Terns (*S. bergii* and *S. bengalensis*).

*Sterna albifrons* probably *saundersi* Hume was rare. I only observed this species once, at Bushire on April 22. There were two specimens together; neither was obtained and no eggs or young were seen.

Of the species of birds proved to breed at the Persian Gulf Hartert (1910–22) does not mention *Phalacrocorax nigrogularis* and *Phaëton aethereus indicus*. In the supplementary volume to this work Steinbacher (1938) gives very short notes about these two species as well as of *Puffinus persicus* as occurring at the border of the palæarctic region. The Shearwater and the Tropic Bird keep to the sea, but the Sokotra Cormorant I should call fairly common or at any rate not rare on the southern coast of Persia. This species is just as palæarctic as *Dromas ardeola, Larus hemprichii, Sterna bergii bakeri* ("*velox*"), *S. b. bengalensis* and *S. repressa* which have all been dealt with in Hartert's book.

Now the winter-visitors and passage-migrants, observed during the time I spent at the Persian Gulf etc., will be mentioned.

*Phalacrocorax carbo sinensis* (Shaw & Nodd.) was very common around Bushire from December 21 till the middle of March, sometimes hundreds being seen. During the next month, which was spent in the southern part of the district, this species was not observed, and when we returned to Bushire on April 14 the birds had left.

Ducks and Geese were very scarce in the saline water. On March 8 I observed a flock of 300–500 *Anas a. acuta* L., some twenty *Tadorna tadorna* (L.) and a few *Branta ruficollis* (Pall.) in a lagoon East of Bushire; apart from these I only saw two *Mergus s. serrator* L., at Bushire on January 18.

*Haematopus ostralegus longipes* But. was fairly common the whole time. The last were seen at Bushire on April 22.

*Squatarola squatarola* (L.) was fairly common till April 5, when the last was seen at the Strait of Hormuz.

*Charadrius dubius curonicus* Gm. was observed twice. A little flock was seen at Larak on March 25 and a pair on Nabiyu Tunb on April 4.

*Charadrius hiaticula tundrae* (Lowe) was only seen at Bushire from December 20–22. A few specimens sojourned near the harbour.

*Charadrius leschenaultii* Lesson was fairly common most of the time. The last was seen at the Strait of Hormus on March 25.

*Eudromias morinellus* (L.). Only one specimen was seen, at Bushire on January 13.

*Numenius a. arquata* (L.) was common. The last were seen at Bushire on April 22. A specimen obtained at the island of Larak on March 28 proved to belong to the typical subspecies.

*Numenius p. phaeopus* (L.) was fairly common. The last flock was observed at Bushire on April 22.

*Limosa l. lapponica* (L.) was seen near Bushire on January 4, only a few birds.

*Tringa totanus eurhinus* (Oberholser) and *Tringa nebularia* Gunn. were fairly common at the inner part of the Persian Gulf. None were observed East of 51° long. E. The last of both species were seen at Bushire on April 22.

*Xenus cinereus* (Güld) was fairly common around Bushire during the first two or three weeks of our stay there; then the birds disappeared. After abt. January 10 only two specimens were seen, one at Bandar Shahpur on February 18 and one at Bushire on April 18.

*Actitis hypoleucos* (L.) was fairly common. The last was seen at the island of Shatwar on April 9.

*Arenaria i. interpres* (L.) was fairly common around Bushire from our arrival till January 22. On February 18 a few were seen at Bandar Shahpur but afterwards none till April 22–25.

*Crocethia alba* (Pall.) was observed now and then, mostly in small flocks. The last was seen at Bushire on April 18.

*Calidris a. alpina* (L.) was fairly common. The last was heard at Bushire on April 22.

*Phalaropus lobatus* (L.) was only seen in April. Small flocks were seen in the Gulf of Oman and the Persian Gulf.

*Stercorarius parasiticus* (L.) was fairly common. The last was seen some miles South of Bushire on April 13. Butler (1877, p. 285) mentions that he saw half a dozen in the Gulf of Oman in the middle of May. I observed both light and dark birds eagerly chasing gulls and terns in the usual way.

*Larus argentatus heuglini* Bree was very common in the inner part of the Persian Gulf from our arrival till we left Bushire about the middle of March. Some were seen in the Strait of Hormuz on April 6, but when we returned to Bushire on April 14 the birds had left this place. From April 26–27 I observed some immature specimens in the northernmost part of the Gulf but no adult ones.

*Larus marinus* L. was only seen near Bushire in January. In the beginning of this month a few stayed at this place. From January 14 to 26 a single adult specimen was seen almost daily at and around the harbour under good conditions of observation. I wanted this bird very much as a proof of the occurrence of this species at the Persian Gulf, but I did not succeed in obtaining it.

*Larus f. fuscus* L. was fairly common at Bushire and Bandar Shahpur in January and February. A single bird (the last observed) was seen at Bahrein on March 17.

*Larus r. ridibundus* L. was fairly common at the inner part of the Persian Gulf till the end of March.

*Sterna s. sandvicensis* Lath. was only observed during spring migration. From March 25 till April 14 this species was common at the Strait of Hormuz and the Persian Gulf.

*Discussion:*

A. Hemmingsen: When travelling in the Society Islands and the Tuamotu Islands in 1939 I thought I noticed differences in the occurrence of the dark and white phases of *Demiegretta sacra*, which made me wonder whether there might be a higher percentage of white specimens in the atolls with light-coloured sand than in the volcanic islands with darker sandy or rocky beaches at least in some places. I never saw a White Heron on the beaches of Tahiti, whereas the dark phase was very common there. I should like to ask whether biotopical differences of this or similar kinds have been observed as regards the two phases of this heron species on the shores of the Persian Gulf.

B. Løppenthin: No ecological difference between blue and grey phase of the Reef Heron. Author saw birds of both colours feeding in different localities.

R. E. Moreau asked for a summary of egg dates as he believed that they were much earlier than the dates in the Red Sea.

B. Løppenthin: Eggs of *Gelochelidon nilotica* were found on April 22; but no other fresh eggs of Gulls, Terns or Waders were seen. Egg dates are certainly much the same as in the Red Sea.

## References

Baker, E. C. Stuart, 1922–30. The Fauna of British India . . . 2nd. ed. London.

—— 1932–35. The Nidification of Birds of the Indian Empire. London.

Blegvad, H., assisted by B. Løppenthin, 1944. Fishes of the Iranian Gulf. Danish Scientific Investigations of Iran, pt. 3. Copenhagen.

Butler, E. A., 1877. Astola, a Summer Cruise in the Gulf of Oman. Stray Feathers, vol. 5; 283–304.

Capito, C. Erik, 1931. Some Birds from the North West Corner of Fars, Persia. Journ. Bomb. Nat. Hist. Soc., vol. 34; 921–35.

Cheesman, R. E., 1925–26. See Ticehurst, C. B.

Cox, Percy Z., 1926. See Ticehurst, C. B.

Cumming, W. D., 1886. See Sharpe, R. Bowdler.

Dickson, Violet, 1942. A Visit to Maskan and Auha Islands in the Persian Gulf, off Kuwait May 7th 1942. Journ. Bomb. Nat. Hist. Soc., vol. 43; 258–64.

Forbes, Henry O., 1899–1903. See Ogilvie-Grant, W. R.

Hartert, Ernst, 1910–22. Die Vögel der paläarktischen Fauna. Berlin.

—— 1932–38. Do. Ergänzungsband. In Gemeinschaft mit Friedrich Steinbacher bearb. Berlin.

Jones, R. Bark, 1946. An Account of a Visit to the Brothers (Jebel Teir) Islands in the Gulf of Aden. The Ibis, vol. 88; 228–32.

Løppenthin, B., 1944. See Blegvad, H.

Oates, Eugene E., 1901–02. Catalogue of the Collection of Birds' Eggs in the British Museum (Natural History), vol. 1–2. London.

Ogilvie-Grant, W. R., and Henry O. Forbes, 1899. The Expedition to Sokotra. 1. Description of new Birds. Bull. Liverpool Mus., vol. 2; 2–3.

—— 1903. The Natural History of Sokotra and Abd-el-Kuri. Birds. Liverpool.

Sharpe, R. Bowdler, 1886. On a Collection of Birds from Fao in the Persian Gulf. With Notes by the Collector W. D. Cumming. The Ibis, ser. 5, vol. 4; 475–93.

—— 1891. Notes on a second Collection of Birds made by W. D. Cumming at Fao in the Persian Gulf. The Ibis, ser. 6, vol. 3; 103–16.

Steinbacher, Friedrich, 1932–38. See Hartert, Ernst.

Ticehurst, C. B., and R. E. Cheesman, 1925. The Birds of . . . Bahrein Island, Persian Gulf. The Ibis, ser. 12, vol. 1; 1–31.

Ticehurst, C. B., assisted by Percy Z. Cox and R. E. Cheesman, 1926. Birds of the Persian Gulf Islands. Journ. Bomb. Nat. Hist. Soc., vol. 30; 725–33.

Witherby, Harry F., 1903. An Ornithological Journey in Fars, South-west Persia. The Ibis, ser. 8, vol. 3; 501–71.

The Persian Gulf Pilot, 8. ed. London 1932.

# Geese in the Canadian Arctic

*Peter Scott*

*Severn Wildfowl Trust, Slimbridge, England*

Until 1938 Ross's Snow Goose *Anser rossii,* with the Bristle-thighed Curlew *Numenius tahitiensis,* was one of the last two North American birds whose nest and eggs had not been found in the wild state. In that year Angus Gavin, a Hudson's Bay Company Post Manager, was shown the breeding ground by the Eskimos of the Kogmuit tribe who live on the Perry River which runs northward into the Arctic Ocean at 102° W.

Gavin made a preliminary report on the breeding of Ross's Goose (Wilson Bulletin Vol. 59, No. 4, Dec. 1947) but much study remained to be done. He also made two important statements which required further examination. He claimed that two forms of the White-fronted Goose *A. a. albifrons,* now *A. a. frontalis* (Todd 1950), and *A. a. gambeli* (the Tule Goose) nested in the region but remained in segregated colonies on separate lakes, and that the Atlantic and Pacific forms of the Brent *B. b. hrota* and *B. b. nigricans* were breeding in the area, but also remained apart, the former nesting on coastal islands, the latter in the marshy delta of the river and along the mainland shore.

For these reasons and in order to make additional studies of the fauna and geography of the region, the Perry River Expedition 1949 was undertaken. It was sponsored by the Arctic Institute of North America. Its three members, Paul Queneau, Harold Hanson and the author, were flown in on skis from Yellowknife, North West Territories, and made camp near the Perry River some 14 miles from its mouth on 6th June 1949. The party returned by float plane by way of Churchill on Hudson's Bay on 4th August. During the last fortnight the float plane (pilot James Bell) was available for aerial exploration, survey and photography.

With the assistance of the eskimos three colonies of Ross's Geese were found, although breeding only took place at one of them, perhaps owing to the exceptional lateness of the season. Some 260 nests were counted in the one colony which occupied 5 islands in a lake. The average brood size of those which successfully hatched was only 2.8. The total stock of the species in this area appeared not to be more than 2 000 individuals including the young birds. It must be remembered that no other breeding area is known, and that the above figure *may* therefore represent the world population of the species.

25 Ross's Geese were ringed and 9 were brought back alive. When examined under the fluoroscope 3 of the 9 were carrying shot.

The Whitefronted Geese in the area were found to be all of one race although the size was unusually variable. Of the 7 collected two males weighed 6 lbs 8 oz and 4 lbs 13 oz. They could not be attributed to *A. a. albifrons* nor yet apparently to *A. a. frontalis.* Neither were they so large as the Tule Goose of California. Further work remains to be done before the nature of the Perry River population of *A. albifrons* can be fully determined.

Only one breeding colony of *Branta bernicla* was studied. It was on one of the coastal islands described by Gavin as the habitat of *B. b. hrota* but consisted of some 28 *B. b. nigricans* with one *B. b. hrota* in company with the Pacific form. It was found that the nest down, descibed by Gavin as a distinguishing feature of the two races was extremely variable among the 14 nests of which all the females were Pacific Brant.

The commonest Goose found breeding in the area was the Tundra Canada Goose *Branta canadensis leucopareia* and a small number of supposedly non-breeding specimens of large Canada Geese, probably attributable to *B. c. moffitti* passed through the area migrating northwards; some of these reappeared after the moult moving southwards.

Lesser Snow Geese *A. c. hyperboreus* were also breeding in small numbers and the only two breeding Blue Geese *A. c. caerulescens* were two males mated in each case to female Lesser Snows. Both males had extensive areas of white on the underparts and flanks. Each mixed brood consisted of two young. In the first case both were yellowish, in the second one was yellowish and the other dusky, (typical of the downy Blue Goose).

Long-tailed Duck *Clangula hyemalis* and King Eider *Somateria spectabilis* were the two most numerous breeding ducks. Pintails, *Anas a. acuta,* were also common but consisted almost entirely of males, and no nests or ducklings were seen.

Preliminary reports of the expedition are published in "Waterfowl Populations & Breeding Conditions, 1949" (U. S. Fish & Wildlife Service and Dominion Wildlife Service of Canada) and the Third Annual Report of the Severn Wildfowl Trust. A full report will be rendered to the Arctic Institute of North America in due course.

The colour film which accompanied this paper showed the general activities of the expedition, the Kogmuit eskimos, and some of the birds, mammals and flowers of the region. The nests, eggs and downy goslings of *Anser rossii* which had not previously been filmed, and of *Anser albifrons* ssp. were shown in close-up.

# The Curlew's Secret

*Arthur A. Allen*

*Cornell University, Ithaca N. Y.*

This kodachrome film, made by Professor Allen, leader of the expedition records the discovery in June, 1948, of the nest and eggs and downy young of the Bristle-thighed Curlew, *Numenius tahitiensis* (Gmelin) about 25 miles north of Mountain Village, Alaska. It shows aerial views of the flight over the Alaska Mountains, the delta of the Yukon River to Igiak Lake, then northward to Curlew Lake. Above this lake, on a plateau behind the coastal range of low mountains the nest was finally discovered by David Allen, accompanied by Henry Kyllingstad, an Alaskan Native Service schoolteacher. The party also included Warren Peterson, another teacher; and the expedition was sponsored by the National Geographic Society and the Arctic Institute of America. The story of the expedition, together with color plates of the Curlew, its eggs and downy young, was published in the National Geographic Magazine December, 1948; and a further discussion of the eggs and young was published by Allen and Kyllingstad in the Auk, Vol. 66, Oct. 1949.

In addition to photographs of the Curlew, the film shows pictures of eleven other species, which may never have been previously photographed in color. The following were included: *Acanthis hornemani exilipes* (Coues), *Philacte canagica* (Sevastianoff), *Motacilla flava alascensis* (Ridgway), *Arenaria melanocephala* (Vigors), *Arenaria interpres morinella* (Linnaeus), *Squatarola squatarola* (Linnaeus), *Phalaropus fulicarius* (Linnaeus), *Arctonetta fischeri* (Brandt), *Grus canadensis canadensis* (Linnaeus), *Falco rusticolus uralensis* (Swertzow and Menzbier), and *Cygnus columbianus* (Ord). Nests and eggs of 34 other species were discovered and photographed, but were not included in the color film.

The expedition reached Alaska May 29, 1948 and returned July first. Specimens of the Curlews, the eggs and the downy young were deposited in the U. S. National Museum and the Laboratory of Ornithology at Cornell University.

# On the Birds of Peter I. Island

*Holger Holgersen*

*Stavanger Museum, Stavanger, Norway*

Peter I. Island was discovered in 1821 by a Russian naval expedition, led by Admiral von Bellingshausen, who sighted the island from a distance of about 20 miles. A few subsequent expeditions have made attempts to reach it, but access was generally rendered impossible by dense and heavy pack ice. The first landing was performed in 1929, when the island was formally occupied for Norway by the second "Norvegia"-expedition. The scientist of the "Norvegia," Dr. O. Olstad, was the first to bring exact news about the birds of the island.

A second landing was made when the Norwegian M/S "Brategg" stayed at Peter I. Island for some days in February, 1948. Being myself a member of the scientific staff of that expedition, I had then some opportunity of studying the birds of this remote island.

Peter I. Island has a very isolated position, 68° 50′ S. lat., 90° 35′ W. long., and is thus lying well within the antarctic circle. The nearest continent is the antarctic mainland, nearly 400 kilometres (210 n. miles) away, and the sea between is practically always covered with ice.

The nearest point of the West Antarctic Archipelago is 550 kilometres (300 n. miles) away, and there are no other oceanic islands in the whole Pacific sector.

The island is about 25 kilometres (15 $^1/_2$ miles) long and 10 kilometres (6 miles) wide. It is entirely covered with snow and ice, no rock being visible except where the slopes are precipitous or the swell washes against the lower parts. The glaciers terminate at the sea in flat ice cliffs similar in appearance to shelf ice. The seaward edge of some of these cliffs appears to be floating, but at others a narrow shelf of bare rock is visible at the water's edge. Lars Christensen Peak, a lofty rounded dome about 1200 metres (4000 ft.) high, is the greatest elevation. There are no harbours.

The Sandefiord Bay, about 3 kilometres (nearly 2 miles) wide, lies on the western side of the island, between Cape Ingrid and Framnes Head. On the latter is a small colony of penguins, consisting in 1948 of 18 or 19 pairs of Adelie Penguin (*Pygoscelis adeliae*) and one pair of Ringed or Antarctic Penguin (*Pygoscelis antarctica*). At the time of our visit in early

February, the Adelies had full-grown chicks, with only some down left on upper parts, head, back, and flippers. At the same time, the two chicks of the Ringed Penguins were only half-grown.—In addition, a single, unmated Ringed Penguin was seen.

Apart from the two penguins, the Silver-grey Fulmar (*Priocella glacialoides*) is the only species known to be breeding, but it is the most abundant bird on the island. Nesting mostly on narrow ledges, it was seen high up on the mountain sides as well as near the sea. Most of the nests lay exposed, others well hidden in the crevices. The nests, or more correctly, nesting birds with their chicks, were only seen on the western side of the island, in groups of 100 up to 800 pairs, not least on the rugged surface of Cape Ingrid, but also on Tvistein, a Bass Rock in miniature off the northwestern extremity of the island.—In all, about 3500 nesting pairs of this species were present.

The Snow Petrel (*Pagodroma nivea*) has been reported as breeding, but the record appears to be erroneous, as the supposed nesting birds seem to have been only the chicks of the Silver-grey Fulmar. The Snow Petrel was, however, present. For instance, a flock of 150 birds roosted on an iceberg off the southern coast one day.

On a platform above Framnes Head and in the immediate neighbourhood of the penguin colony, two South Polar or Maccormick's Skua (*Catharacta skua maccormicki*) landed repeatedly. One of these was secured and proved to be a male. The other one may have been a female, with young on the above-mentioned platform, which we were unable to reach.

Wilson's Petrel (*Oceanites oceanicus*) was constantly seen off the western coast, and must have been present in some 60 specimens or more. Several birds could be observed at any time fluttering above Framnes Head, where they now and then disappeared in the rock crevices. It may be regarded as not impossible that they nested there.

Other species observed were Stinker or Giant Fulmar (*Macronectes giganteus*), of which three specimens were seen, two young birds and one adult of the white phase, the Antarctic Petrel (*Thalassoica antarctica*) and the Cape Pigeon (*Daption capensis*), both of which were seen in only single or a few specimens now and then.

Terns were seen very often, flying or resting on the ice. Some of them were adults with a complete black cap, whilst others—and most of them—had a white or mottled black and white forehead. They were very shy, and we did not succeed in securing any specimens, but Dr. Olstad in 1929 shot an Arctic Tern (*Sterna paradisaea*) at the island.

With its isolated position, Peter I. Island might be supposed to form an important nesting site for several species, and be a stronghold for antarctic bird life. But—as already indicated—this is not the case, bird-life is poor. One reason may be that the ocean in which it lies, is sparsely provided with the marine organisms, which form the principal food of the birds in question, as compared with other parts of the southern sea. Another is that the island offers only limited and unfavorable nesting grounds.

To conclude, we can summarize our present knowledge of the avifauna of this island as follows:

Three species have been definitely stated as breeding, two penguins and one petrel. Two others may possibly breed, a skua and a petrel. Five species, including four petrels and a tern, have been observed repeatedly along the coasts, and whalebirds (*Pachyptila* sp.) and two albatrosses have been observed at some distance, but well within eyesight of the island.

In all, this gives a total of only thirteen species, a remarkably low figure, but among these species we find some of the most hardy birds of the world, adding life to a desolate antarctic island.

Our present knowledge of the avifauna of Peter I. Island:

| | | |
|---|---|---|
| Adelie Penguin | *Pygoscelis adeliae* | breeding |
| Ringed Penguin | » *antarctica* | » |
| Silver-grey Fulmar | *Priocella glacialoides* | » |
| South Polar Skua | *Catharacta skua maccormicki* | Possibly breeding |
| Wilson's Petrel | *Oceanites oceanicus* | » » |
| Giant Fulmar | *Macronectes giganteus* | Observed |
| Cape Pigeon | *Daption capensis* | » |
| Snow Petrel | *Pagodroma nivea* | » |
| Antarctic Petrel | *Thalassoica antarctica* | » |
| Arctic Tern | *Sterna paradisaea* | » |
| Whale-bird | *Pachyptila* sp. | » |
| Black-browed Albatross | *Diomedea melanophris* | » |
| Light-mantled Sooty Albatross | *Phoebetria palpebrata* | » |

## References

Davis, M., 1949. Extension of the range of the ringed penguin. Auk 66. Lancaster.

Holgersen, H., 1945. Antarctic and Sub-Antarctic Birds. Sci. Res. Norw. Ant. Exp. 1927–1928 et Sqq. No. 23. Norske Vidensk. Akad. Oslo.

—— 1949. Den norske sydishavsekspedisjon 1947–1948. Naturen Nr. 12. Bergen.

—— (1951). Range of the ringed penguin. Auk 68 (in press).

—— (Ornithology of the "Brategg" expedition 1947–48, in preparation.)

Olstad, O., 1929. Trekk av Sydishavets dyreliv. Norsk geogr. tidsskr. II, h. 8. Oslo.

Tofte, E., 1927. "Odd I"s tokt til Peter den Förstes Ö. Ibidem I.

# Birds of Tristan da Cunha

*Yngvar Hagen*

*Jelöy, Moss, Norway*

The Norwegian Scientific Expedition to Tristan da Cunha 1937–1938, in which I took part, arrived at the group on December 7th and stayed until March 29th. Some time was spent on each of the 3 islands, Tristan itself, Nightingale and Inaccessible. Since the war, other observers have visited Tristan da Cunha, and recent data is published by Roberts and by Broekhuysen & Macnae in 1948 and 1949.

I shall give a revision of the Tristan avifauna together with short comments.

Until the Norwegian expedition in 1937 started to survey these islands, 36 different species of birds had been included in the Tristan fauna. A critical treatment of the matter made it certain, however, that species of birds had been listed, which actually had never been proved to belong to the fauna. Further, synonyms had been mistaken for different species.

It must be wrong that the Grey-backed Stormy Petrel, *Garrodia nereis* Gould, has been recorded from Tristan, and may only be explained by the single specimen found by Wilkins at Gough Island in 1922. That the Black-bellied Stormy Petrel, *Fregetta tropica* Gould belongs to the Tristan fauna, is not yet proved. The *Fregettornis melanoleuca* Salvadori proves to be identical with the special Tristan-race of the White-bellied Stormy Petrel *Fregetta grallaria* Vieillot.

Thus—of the 36 species listed by G. M. Mathews—only 33 are correct and stand a critical revision. On the other hand 3 species, new to the fauna, have been recorded more recently, though only as accidental visitors. Thus, in the ultimate list of the Tristan avifauna, there are now 36 species of birds.

The Macaroni Penguin, *Eudyptes chrysolophus* Brandt, captured by me at Inaccessible on March 3rd 1938, is new to the fauna.

Biological and physiological studies were made of the Rockhopper Penguin, *Eudyptes crestatus* Miller, and the position of the rookeries was mapped. An attempt was made to clear up the oceanic wanderings of this species, through the banding of 532 individuals. However, the result was quite negative, as not one single recaptured penguin has been reported in 12 years. In a letter from Mr. and Mrs. Rowan, however, who stayed for 9 months on Tristan da Cunha in 1949, it is mentioned that ringed penguins are still to be found on Tristan itself during the breeding season. Exact records are lacking.

A record of the Light-mantled Sooty Albatross, *Phoebetria palpeprata* Forsteri, as new to the Tristan fauna, was published by Roberts in 1948.

The Sooty Albatross, *Phoebetria fusca* Hilsenberg, breeds on all the 3 islands in the group, but was nesting solitary, not in colonies.

Regarding the Wandering Albatross, *Diomedea exulans* Linné, I leave the solution of the confused nomenclature of its subspecies to the future, though I have here chosen to follow Murphy, calling the Antarctic Wandering Albatross *Diomedea exulans exulans* Linné and the Tristan race *Diomedea exulans dabbenena* Mathews. However, the alternative of regarding the Linnean type from the Cape Seas as representing the larger antarctic form (instead of the Tristan form) is opposed by Falla. I met with both races in the Tristan waters, and the race *dabbenena* still breeds on the high plateau of Inaccessible.

The Black-browed Albatross, *Diomedea melanophris* Temminck, is an annual visitor, coming in March.

The Yellow-nosed Albatross, *Diomedea chlororhynchos* Gmelin, breeds in dense colonies at Nightingale and more scattered elsewhere in the group. Biological and physiological studies were made, but I confine myself to giving the banding results here. In 1938 a total of 570 mollymawks of this species were banded, mostly young birds and chiefly in February at Nightingale, where the colonies offered a sufficient density of individuals for ringing on an effective scale. The rings, which were returned, were in all 23, of which 12 were from outside the Tristan group (Fig. 1). They came exclusively from individuals which were juveniles in 1938, and of those the first one was captured off Walvis Bay on April 17th the same year. This is remarkably soon, as the juveniles first reach their fledgling stage at the middle or towards the end of March. Only 3 days later, April 20th, one reached Mossamedes in Portuguese Angola and thus had advanced straight into the Tropics. On April 24th another one was recorded off Walvis Bay, but after this date only Mossamedes-records occurred,—one undated said to be obtained early in the season of 1938, 1 in June that year, 3 in August, 1 in September, 1 in October and two in November. The latter cases are remarkable ones, because, as the breeding season starts in September, they indicate that at least a precentage of the yearlings do not partake in the

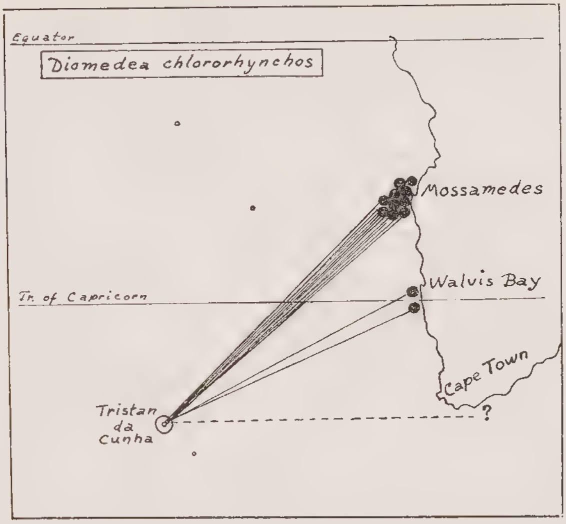


Fig. 1. *Diomedea chlororhynchos* ringed at Tristan da Cunha in 1938 and recovered off the African coast.

reproduction. In spite of these quite numerous records of immature birds in the first southern winter, there are absolutely none from outside Tristan da Cunha from the second or any later year (apart from a doubtful case at Knysna in South Africa in 1942). From the breeding ground, however, there are more records. There were 3 bands taken from mollymawks on Nightingale in February 1946 by Mr. John Kirby. At the end of September 1949, after nearly 12 years, no less than 8 ringed mollymawks were identified on Nightingale. I quote Mrs. Rowan's letter: "In the first . . . Pond we found six banded birds . . . of which 3 were incubating eggs, and all had nests. . . . In the second . . . Pond we found two banded birds, nesting . . . . The first was performing courtship ceremonies . . . with an unbanded bird . . . . The second was incubating an egg." Exact figures, read from the rings, follow each of these pieces of information.

The Giant Petrel, *Macronectes giganteus* Gmelin, does not breed in the Tristan group. However, it bred there during the last century in a rookery at Bull Point on the Tristan main island until about 1870. The birds were attracted by the annual slaughtering of Sea-Elephants, which regularly came on shore then, until the greater part of these mammals were exterminated in the Tristan waters. Single Giant Petrels are still observed round the islands.

The Broad-billed Whalebird, *Pachyptila forsteri* Latham, breeds in the group.

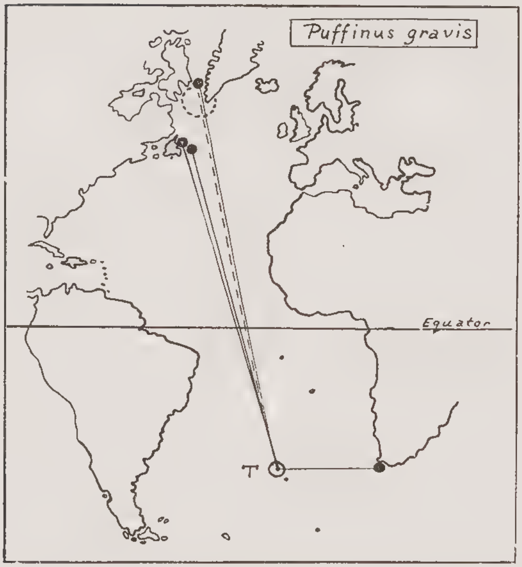


Fig. 2. *Puffinus gravis* ringed at Nightingale in the Tristan group in 1938 and recovered off South Africa, New Foundland and Greenland.

I observed the white-chinned form of the Shoemaker, *Procellaria aequinoctialis aequinoctialis* Linné at Tristan, but it does not breed on the islands. The local name is "Cape Hen." However, the spectacled form, *Procellaria aequinoctialis conspicillata* Gould, breeds on the high plateau of Inaccessible. Here I observed 7 specimens (of which 5 were collected), and all the representatives of this minute population were of the *conspicillata* type. The Tristanites call this bird "Ring-Eye" and thus recognize it as a bird differing from the normal white-chinned form. The sub-specific value of *conspicillata* has been doubted among ornithologists, but now, when this form has been geographically localized, I think *conspicillata* might be considered as a good race.

The Greater Shearwater, *Puffinus gravis* O'Reilly has a breeding stock roughly estimated at about 1 million birds on Nightingale. The population on Inaccessible is much smaller, and whether it breeds on Tristan itself is unknown. Biological and physiological studies were made, but here only the banding results should be referred to. A total of 811 birds, practically all adults, were ringed at Nightingale in 1938. Only 5 rings were returned during the course of 3 years (Fig. 2). The 2 first birds came from New-Foundland waters, recaptured on June 15th and 20th in the same year as banded. The 3rd was recorded off Godthåb on the West Coast of Greenland on the 4th of August in the same year. The 4th also came from Greenland waters, probably in the summer of 1939. Then, finally, "in the spring" of 1940 one was recaptured at George, Cape Colony, South Africa. Concerning the two latter, exact data are lacking.

The Pediunker, *Adamastor cinereus* Gmelin, the Long-winged Petrel, *Pterodroma macroptera* Smith, the Atlantic Petrel, *Pterodroma incerta* Schlegel, the Soft-plumaged Petrel, *Pterodroma mollis* Gould as well as the Diving Petrel, *Pelecanoides urinatrix* Gmelin, are all breeding in the Tristan group, though all of them in fairly small numbers.

The White-faced Stormy Petrel, *Pelagodroma marina* Latham occurs in some abundance at Tristan da Cunha, and obviously breeds there too, though actual egg-records are still lacking.

The White-bellied Stormy Petrel, *Fregetta grallaria* Vieillot, is clearly a resident of the Tristan group. Actual breeding records were made for the first time by me in February 1938, as eggs were found at Nightingale. There has been some doubt as to whether the Tristan White-bellied Stormy Petrel represents a race of its own. The series obtained by the Norwegian expedition removes the doubt, but, at the same time reveals that the Tristan form is described by Salvadori in 1908 under the specific name of *Fregetta melanoleuca*, while the race has to be called *Fregetta grallaria melanoleuca*. The *Fregetta grallaria tristanensis* of Mathews 1932 is then a synonym.

The Tristan Skua, a form of the species *Catharacta skua* Brünnich, is occasionally simply considered as a subordinate population of the Brown Skua, *Catharacta skua lønnbergi*, sometimes thought to be identical with the Falkland Skua, *Catharacta skua antarctica*, sometimes, as by Murphy, considered as a race of its own, though hitherto only designated as *Catharacta skua* subspecies by him. Based on the material obtained by the Norwegian expedition as well as on the careful study of Hamilton's, I propose to give it a subspecific name, *Catharacta skua hamiltoni, subsp. nov.* The Tristan Skua resembles both the Brown Skua in the south, the Falkland Skua in the west and the Great Skua, *Catharacta skua skua* of the north, however, being none of them, standing in an intermediate position.[1]

The Tristan Tern, *Sterna vittata tristanensis* Murphy, is a breeding resident of the Tristan group.

The Brown Noddy, *Anoüs stolidus* Linné, breeds on all the 3 islands in the group. On the other hand there seem to be no records of the Black Noddy, *Anoüs minutus* Boie, since the "Challenger" expedition. However, the local name for the noddies in the Tristan group: "Wood-Pigeon," suits the brown Noddy too, as that species is actually represented by two ecologic races, one breeding on cliffs, another building pigeon-like nests of twigs in the branches of the trees. I collected several samples of such tree-nesting noddies, and found that they were all typical *Anoüs stolidus* Linné.

---

[1] See footnote next page.

The Tristan Bunting, *Nesospiza acunhae* Cabanis, is endemic to the Tristan group, occurring in 2 now-living races, the *Nesospiza acunhae questi* Lowe on Nightingale, and another race on Inaccessible. Whether this latter is identical with the type of Cabanis' *Nesospiza acunhae acunhae,* probably can not be decided. So far no representative series exists of the typical race which once lived on the Tristan main island, but is now extinct there. Studying plumages of moulting *Nesospiza acunhae* I could prove that the juvenile type of pattern is retained in the successive plumages during the second and third year of life, while the birds with mature plumage probably have to be several years old.

The endemic Wilkins' Bunting, *Nesospiza wilkinsi* Lowe, occurs both on Nightingale and Inaccessible. The Inaccessible form differs clearly from the Nightingale bird and has to be described as a new subspecies. I have called it *dunnei, subsp. nov.,* in honour of the geologist member of the Norwegian expedition, J. C. Dunne, as he was the first to rediscover this bird on Inaccessible.[1]

The typical race of the Tristan Thrush, *Nesocichla eremita* Gould, is still living on the Tristan main island, though in small numbers. 5 specimens were collected. The thrushes living on Nightingale and Inaccessible resemble each other completely, but differ clearly from the typical *eremita.* This is why Stenhouse in 1924 described these birds as a race: *Nesocichla eremita gordoni.*

An American Barn Swallow, *Hirundo erythrogaster* Boddaert, shot by the Tristan Settlement on March 22nd 1938, is new to the fauna.

The American Purple Gallinule, *Porphyrula martinica* Linné, is a regular visitor on Tristan da Cunha, which might be a little surprising. The resident people have also given a name to it, viz. "Gutter-Snake."

The endemic flightless Rail, *Atlantisia rogersi* Lowe, occurred abundantly on Inaccessible in 1938, and according to Broekhuysen & Macnae, it does so still. The interesting problems which have arisen owing to the existence of flightless ralline birds on oceanic islands, cannot be discussed in this short lecture. I should only emphasize that *Atlantisia* has clearly developed from a flying ancestor, as concluded by Stresemann in 1932, and confirmed by Sick in 1937. Studies of this bird seem to reveal another feature in this species which might be of interest, namely that the fertility —through adaptation—has considerably decreased. This is probably manifested partly through a prolongation of the immaturity stage to comprise more than 1 year, partly through the existence of non-breeding mature individuals, and the small clutch of two eggs. This slow reproduction is, however, not peculiar to *Atlantisia,* but parallels the conditions in some of the other endemic birds in the Tristan group. As a matter of course, the reproduction, as it frequently does in oceanic islands, has become low in order not to cause excess of population. I am, myself, not familiar with such problems, but so far the prolonged immaturity in *Atlantisia* must be a result of a secondary adaptation to insular conditions, it cannot have any phylogenetic significance.

---

[1] As details concerning the new subspecies cannot be given here, those who are interested should be referred to my paper "Birds of Tristan da Cunha," which will be printed this year in "Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937–38." Videnskaps-akademiets Skrifter, Oslo.

However, there still remain interesting arguments touching this problem (origin of flightless rails). To mention one of them, I should point out the fact that Ascension Island, by the geologists assumed to be comparatively young, according to Kinnear also had its flightless rail. However, this has been extinct for several hundred years.

*Discussion:*

G. Kramer: Did the birds of the rock-breeding colony of Noddies have the opportunity of building their nests in trees, and vice versa, did the tree-breeding birds have the opportunity of breeding on rocky ground?

Y. Hagen answered he was not sure about that.

R. C. Murphy asked whether the Macaroni Penguin and the Giant Fulmar had ever been recorded as nesting birds at Tristan, or merely as casual visitors ashore.

Dr Murphy then spoke briefly on the zonal correlations in the breeding ranges of several sea-birds in both the South Atlantic and the New Zealand area.

He added that the endemic *Porphyriornis nesiotis* of Tristan still survives, and that a specimen of a young bird had recently been received in New York.

Y. Hagen: Only one single specimen of the Macaroni Penguin was found — an accidental visitor. The Giant Fulmar bred there during the foregoing century.

## References

Broekhuysen, G. J. & W. Macnae, 1949. Observations on the birds of Tristan da Cunha Islands and Gough Island in February and early March, 1948. — Ardea, 37, 1–2: 97–1.

Cabanis, 1873. Journ. f. Orn. 1873, (p. 154) Berlin.

Challenger, The Voyage of H. M. S.: See Moseley, Sclater.

Christophersen, E., 1947. A short Account of the Expedition: Results of the Norw. Sci. Exp. to Tristan da Cunha 1937–1938. Vol. I. Det Norske Videnskaps-Akademi i Oslo. (pp. 1–24).

Falla, R. A., 1937. Birds. — B. A. N. Z. Ant. Res. Exp. 1929–1931. Reports, Ser. B., 2. Adelaide.

Hamilton, J. E., 1934. The Sub-Antarctic Forms of the Great Skua (*Catharacta skua skua*). — Discovery Reports, 9. Cambridge.

Kinnear, N. B., 1935. Zoological Notes from the Voyage of Peter Mundy, 1655–56 (a) Birds. — Proc. Linn. Soc., London. Session 1934–1935.

Lowe, P. R., 1923. Notes on some Land Birds of the Tristan da Cunha Group collected by the 'Quest' Expedition. — Ibis, Ser. 11., 5. London.

—— 1928. A Description of *Atlantisia rogersi* with some Notes on flightless Rails. — Ibis, Ser. 12. 4. London.

Mathews, G. M., 1932. Birds of Tristan da Cunha. — Novit. Zool., 38, 1 (Tring). London.

Moseley, H. N., 1879. Notes by a Naturalist on the 'Challenger'. London.

Murphy, R. C., 1936. Oceanic Birds of South America. I & II, 1245 pp. New York.

—— 1938. On Pan-Antarctic Terns. Birds collected during the Whitney South Sea Exp., XXXVII. — Amer. Mus. Novit., No. 977. New York.

Norwegian Sci. Exp. to Tristan da Cunha 1937–1938: See Christophersen.

Roberts, A., 1948. On a Collection of Birds and Eggs from the Tristan D'Acunha Islands, made by John Kirby. — Ann. Transv. Mus., 21, 1.

Salvadori, T., 1907. (On *Fregetta melanoleuca*, n. sp.) — Bull. Brit. Orn. Club, 21.

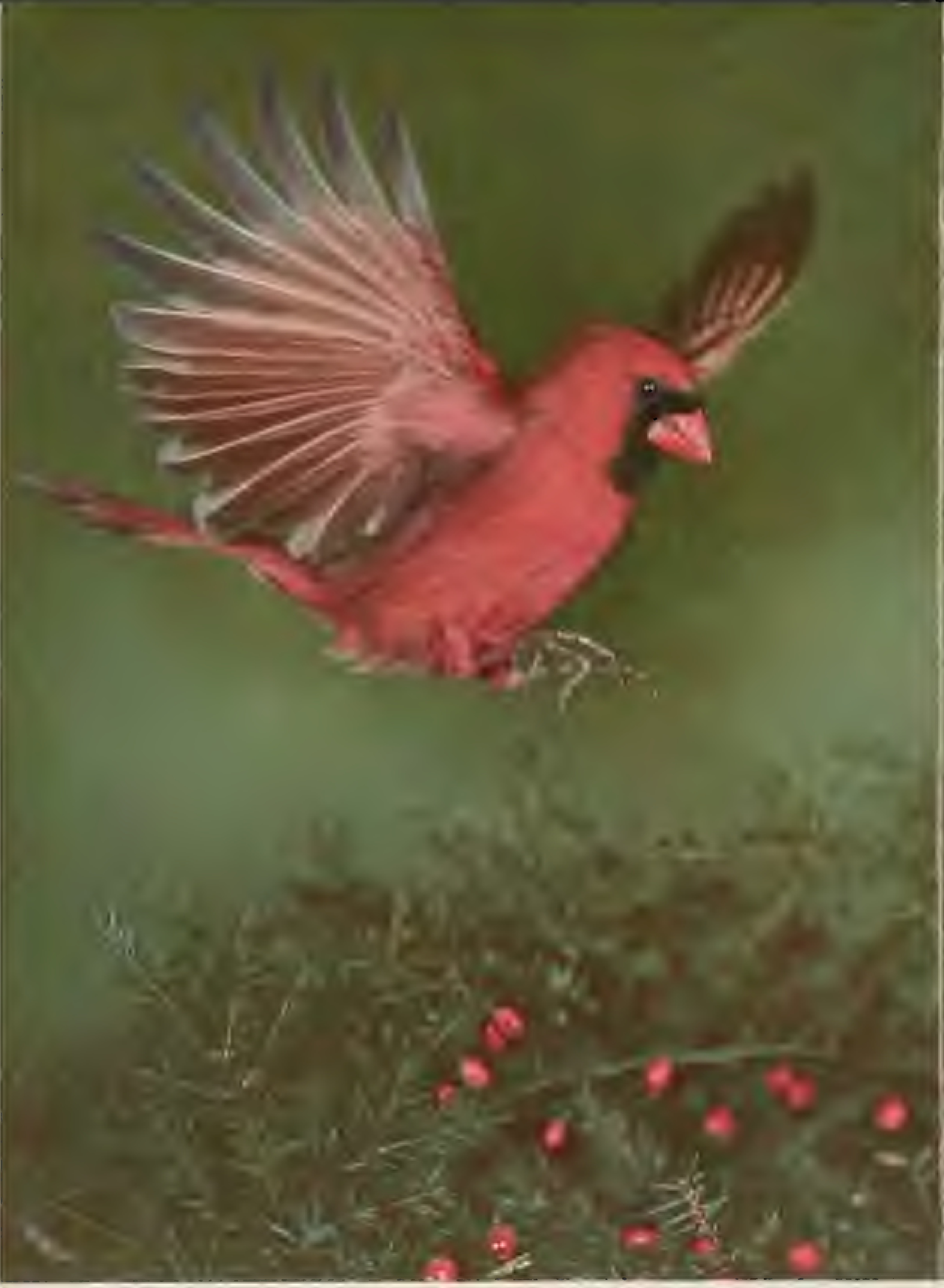
Sclater, P. L., 1881. On the Birds collected on the Atlantic Islands and Kerguelen Island, and on the Miscellaneous Collections. — Rep. Sci. Res. Voy. 'Challenger', Zool. 2. London/Edinburgh.

Sick, H., 1937. Morphologisch-funktionelle Untersuchungen über die Feinstruktur der Vogelfeder. — Journ. f. Orn., 85. Berlin.

Stenhouse, J. H., 1924. Notes on rare Land Birds from Tristan D'Acunha in the Royal Scottish Museum. — The Scottish Naturalist No. 147. Edinburgh.

Stresemann, E., 1932. La Structure des Remiges chez quelques Râles physiologiquement aptères. — Alauda, 4.

Wilkins, G. H., 1923. Report on the Birds collected during the Voyage of the 'Quest' (Shackleton-Rowett Expedition) to the Southern Atlantic. — Ibis, Ser. 11, 5. London.



Eastern Cardinal *Richmondena cardinalis cardinalis* (Linnæus) caught in midair with the speed flash at 1/5,000 of a second. (c) Kodachrome by Arthur A. Allen. Courtesy of the National Geographic Society.

# Progress in Bird Photography and Sound Recording

*Arthur A. Allen*

*Laboratory of Ornithology, Cornell University, Ithaca N.Y.*

At the last International Congress, held at Rouen in 1938, it was my privilege to report on the Cornell-American Museum Expedition for photographing and recording the voices of rare and vanishing birds.

At that time we had recorded on film what we thought were satisfactory renderings of 247 species of North American birds and a few calls of amphibians and insects. We had photographed in black and white 302 of the 815 species on the A. O. U. Check-List.

In the intervening twelve years there has been much progress in sound recording and in photography, such that we have started all over again—first in recording, with an improved 16 mm Bernt-Maurer sound recorder, and next, when invited by the U. S. Army to identify and record Jungle sounds, with a Presto disc recorder. More recently we have secured a Presto Magnetic tape recorder and this recorder gives promise of being the best of all. The new score on birds recorded is 335 of those in the A. O. U. Check-List, 200 Panamanian jungle sounds, including birds, mammals, amphibians, insects, etc. and 33 of the birds of Mexico. We have photographed 583 of the Check-List birds, including 352 in color. We have set up at Cornell what we call a "Library of Natural Sounds," and have published under the name of the A. R. Brand Bird Song Foundation, an album of six records with 72 bird songs and another album of four records with 26 amphibian calls—all on standard vinylite records. Mr A. R. Brand, who started the bird song recording project at Cornell, published his first records in 1934 and 1936, and these were considered excellent at the time and altogether contained 80 songs.

Since that time, bird song recording has progressed in other countries as well as in the United States, and especially in Sweden, where under the direction of Sture Palmér, the Radiotjänst has issued since 1937, 65 records with the songs and calls of 170 species—a remarkable achievement. In

England, Nicholson and Koch have published two series of records, including 75 species, the first in 1936. In 1949, the British Broadcasting Corporation processed recordings of 116 species by Ludwig Koch. In 1936 Oscar Heinroth in Germany published, with his book, three records, including the songs of 22 species recorded by Ludwig Koch. In Denmark, Carl Weismann, starting in 1934, published his first record in 1939, and now has eight records, including the voices of eight mammals, ten frogs and 57 birds. A number of other scattered records have come to our library, like the recording by Ray Littlejohn in Australia of the Lyre Bird (in 1931), and there are, doubtless, others, such as those of the Australian Broadcasting Co. (8 records) and those of the Public Relations Bureau of the Colony of Mauritius which we have not seen, but which we would very much like to include in the Cornell Library of Natural Sounds.

So far as the color photography of birds is concerned, we have enjoyed very pleasant associations with the National Geographic Society, which has sponsored the project and made it possible for me to visit many of the interesting ornithological spots in North America from Florida to Labrador and from California to Alaska. Many hundreds of photographs have been secured on 35 mm Kodachrome film, representing over 350 species of birds. Of these about 150 birds, together with 23 of frogs, have thus far been published in the National Geographic Magazine. The birds photographed do not always coincide with those recorded, but it is our hope and expectation to have a photograph in natural color to match each bird whose voice has been recorded, so that they can be used together.

The most outstanding progress in bird photography since the last International Ornithological Congress in 1938 has been in the development of color and speed. Photographs that were considered impossible in 1938 are now commonplace. There still remains room for improvement in the speed of color films and in the quality of the sound track on such films as Kodachrome and Ansco, but the motion picture films shown at this Congress are a great improvement over those of 1938, because of their natural colors, though the portrayal of bird behavior and action are much the same. In the realm of still life photography, there has been some progress in the increased use of color. The most conspicuous advance has been made in the use of the speed flash, both for black and white and color, such an advance that the ordinary flash bulbs have been outmoded, and even sunlight itself no longer gives results comparable to the flash.

The flash apparatus, which produces the light of tremendous power, but of very short duration, consists, in simplest terms, of a battery or other electric power source, a means of changing the low voltage to 2 000 or more volts and of storing the energy in a condenser until it is ready to be discharged through a vapor-filled tube in the incredibly short space of time of 1/5 000 or even 1/10 000 of a second. Indeed, large laboratory equipment can produce powerful flashes of one-millionth of a second duration. The flash is synchronized with the shutter set at 1/200 or 1/400 of a second, and the amount of actual sunlight admitted, with the diaphragm shut down to the correct stop, is normally too insignificant to affect the film.

This apparatus and its use in bird photography, as well as in a great variety of other projects, was first demonstrated in 1939 by Dr. Harold E. Edgerton, of the Massachusetts Institute of Technology, in his book, "Flash," and later in the National Geographic Magazine for August, 1947, with some marvellous Hummingbird photographs in color. During the past three years, a number of ornithologist photographers in several countries, have added the speed flash to their equipment and produced "stop-motion pictures" of unbelievable beauty and interest, both in color and in black and white. These give us a new insight into the use of birds' wings and wing feathers, as well as the postures of tail and feet in small birds during flight, that was formerly impossible to see. One of the color photographs made by the author with this apparatus accompanies this article. It was first published in a series appearing in the National Geographic Magazine for June, 1948. In 1949 Eric Hosking and Cyril Newberry published their book, "Birds in Action," containing a beautiful selection of speed flash pictures of English birds, some in color.

Up to the present time the sound track on Kodachrome motion picture film has not yielded very great fidelity for the higher frequencies of bird songs, but there is promise of great improvement in the near future. Therefore, instead of showing at the Congress some of our experimental Kodachrome motion picture films with the synchronized songs, a few of our phonograph records will be played, with matching 35 mm slides, similar to the photographs that have appeared in the National Geographic Magazine, together with a few others from various parts of North America, which will probably be published in the not too distant future.

(Followed by the songs of 18 birds from the Album of American Bird Songs with synchronized 35 mm Kodachrome slides; these, in turn, followed by 50 Kodachrome slides of typical American birds, photographed from Florida to Alaska; a number of them by means of the speed-flash equipment.)

# The Moa Deposits of Pyramid Valley Swamp, New Zealand

*Robert Cushman Murphy*

*American Museum of Natural History, New York*

The remarkable skeletal deposits in the bed of a fully silted post-glacial pond occupying a corrie-like depression between limestone ridges near Waikari, North Canterbury, were first reported upon shortly before all field work was interrupted by the war (Allan, R. S., E. Percival, R. S. Duff, R. A. Falla, Records Canterbury Mus., 4: 325–353, 1941.) In 1947 and 1948, excavations planned and supervised by Roger S. Duff, Director of the Canterbury Museum, Christchurch, were resumed, and the writer had the privilege of participating as a representative of the American Museum of Natural History during both seasons.

Operations were conducted by digging and thoroughly searching successive 4-meter squares, all soil being removed to the lowest ossiferous layers, which were rarely more than 2 meters below the surface. Sampling of numerous quadrats indicated an average of perhaps 700 skeletons of moas and other large birds per acre throughout an area of ± 4 acres. The fact that the birds died as a result of miring and rapid engulfment in the sticky bed of the pond has resulted in an extraordinarily high proportion of integrated skeletons. It is in this respect that the Pyramid Valley Swamp differs from most or all previously worked deposits.

Cross sections of the swamp show that the present black humous surface was duplicated at an earlier period by a similar surface now lying beneath more than a meter of organic "swamp dough," which emits a strong odor of hydrogen sulfide (Figure 1). The surface now at ground level is a thick humus of forest origin, although Pyramid Valley throughout historic time has lain near the center of a grassland area with an annual precipitation of less than forest requirements. The strata thus reflect successive cycles of post-glacial climate in South Island which are known from other evidence of several types. The layers have not yet been dated, but toward this goal studies of pollen and of the included mollusks and other invertebrates are now being prosecuted in New Zealand and elsewhere.

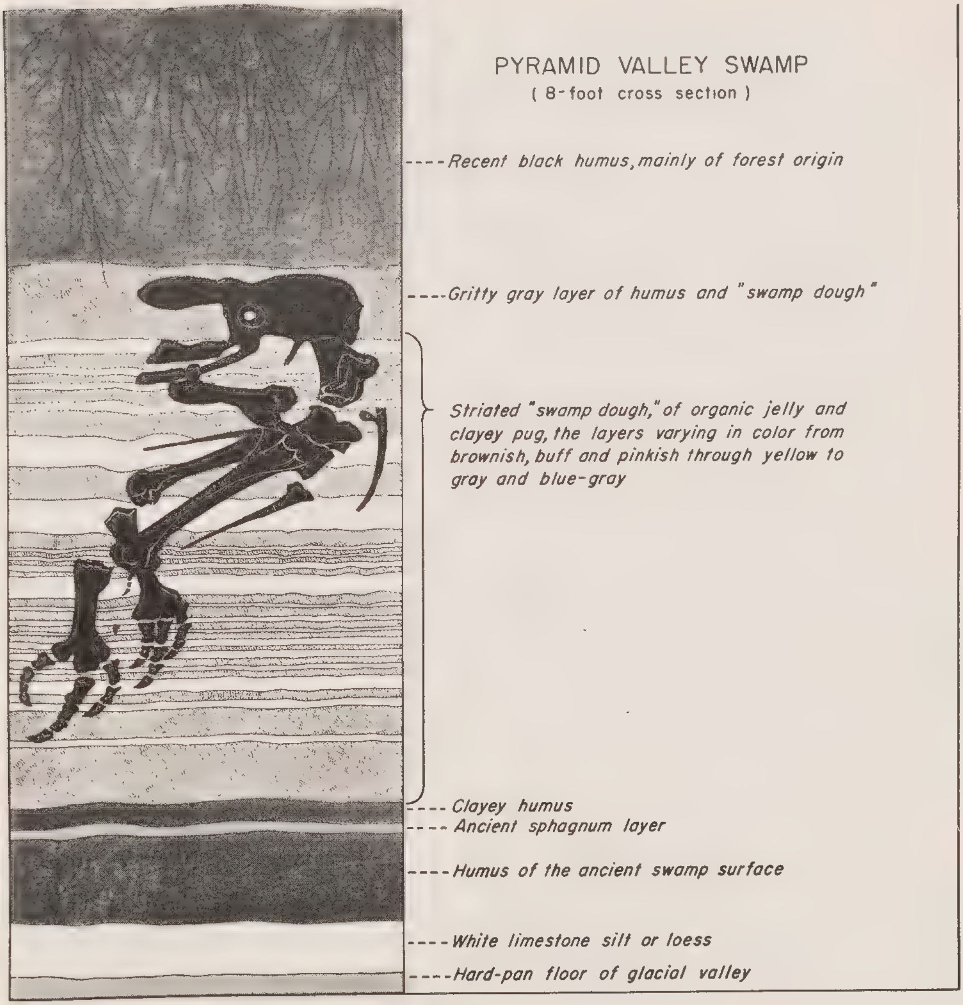

PYRAMID VALLEY SWAMP
( 8-foot cross section )
Recent black humus, mainly of forest origin
Gritty gray layer of humus and "swamp dough"
Striated "swamp dough," of organic jelly and clayey pug, the layers varying in color from brownish, buff and pinkish through yellow to gray and blue-gray
Clayey humus
Ancient sphagnum layer
Humus of the ancient swamp surface
White limestone silt or loess
Hard-pan floor of glacial valley

Fig. 1. Vertical cut bank of Quadrat 73, Pyramid Valley swamp, drawn from measurements and kodachrome photographs. Superimposed is a sketch of part of a complete skeleton of *Emeus*, as it was stratigraphically distributed in a neighboring but earlier excavation.

Entrapment of the large birds was not, of course, simultaneous. Accumulated skeletons of the moa genera *Dinornis, Pachyornis, Emeus* and *Euryapteryx,* each represented by one or more species, probably cover a period of several or many thousand years. The individual catastrophes to the birds seem to have been a result of cracking through a more or less firm surface upon which they had entered in search of vegetable food such as the drupes of podocarp trees. A considerable variety of fruits and foliage of New Zealand plants still extant, though no longer flourishing in the North Canterbury grasslands, has already been identified in the abundant stomach contents of the more deeply buried moas.

Neither skin, feathers, nor other soft tissues remain in the anaerobic organic jelly that has kept bones and ingested vegetation intact and perfect. The presence of stomach contents with some skeletons, and its absence in other instances, may relate in part to the speed with which death ended the struggles of entrapped birds. The only instances of disintegration due to weathering of bones are confined to the uppermost humous layer. Material thoroughly enclosed in the jelly is in "laboratory condition," even though drifting or other stresses have in frequent instances scattered the bones of individual skeletons. Heads and necks are the parts most often missing or separated by a distance that prevents primary association.

Aside from the disclosure of a peerless morphological record, the Pyramid Valley investigations, which are now continuing, are destined to throw much new light upon the behaviour, ecology, and life history of the Dinornithidae and other birds of ancient New Zealand. Their food and eggs, their growth stages from chick to adult, the contemporary fauna and flora of their final period and their enemies, such as the extinct vulture-eagle *Harpagornis,* are all being recovered in association with the moa bones.

# Über eine Rekonstruktion des Schädels von Archaeornis siemensi Dames 1884 im Naturhist. Museum, Braunschweig

*Adolf Kleinschmidt*

*Naturhist. Museum, Braunschweig*

Bekanntlich sind von den Archaeopteryges zwei Typen aus dem weissen Jura von Solenhofen bekannt:

*Archaeopteryx macroura* Owen 1863, dessen Original sich in London befindet, und

*Archaeornis siemensi* Dames 1884, dessen Original s. Zt. für Berlin erworben wurde, und über dessen Verbleib nach dem 2. Weltkrieg leider Unklarheiten bestehen.

Nur von letzterem ist der Schädel überliefert. Beide sind aber schon stark differenzierte Formen, wie die Untersuchung der Becken gezeigt hat.

Angeregt durch die Notwendigkeit einer musealen Darstellung der Entwicklungsgeschichte der Vögel, im besonderen der der Archaeopteryges, habe ich mich auf Grund der Arbeiten von Heilman mit dem Problem der plastischen Rekonstruktion des gesamten Archaeornis-Schädels befasst.

Ich ging hierbei in erster Linie von den Darstellungen aus, die Heilman in seinem Buch Origin of birds (1926) gegeben hat. Nach der dortigen Seitenansicht des Schädels wurde eine Rekonstruktion der ja zum grössten Teil im Original vollständig verdeckten palatinalen Unterseite, des Kiefer-Gaumen-Apparates versucht, die ja bei weitem das schwierigste Problem für die gestellte Aufgabe darstellte.

Tatsächlich sind nach den Angaben von Heilman aber trotz allem soviel Einzelheiten sichtbar, dass man wohl diesen Versuch wagen und auch die Umrisse des Gehirnschädels im besonderen und damit eine ungefähre Hirngrösse festlegen konnte. Eine wesentliche Voraussetzung war hierbei, dass erst einmal der in der Orbita befindliche Skleralring ,,fortgenommen“ wurde, da er das Blickfeld behindert.

Ich ging nun so vor, dass ich sorgfältige Pausen der Seitenansicht in fünffacher Vergrösserung fertigte, auf denen die mutmasslichen Knochengrenzen nach Heilman eingetragen wurden. Ausserdem wurden die einzelnen

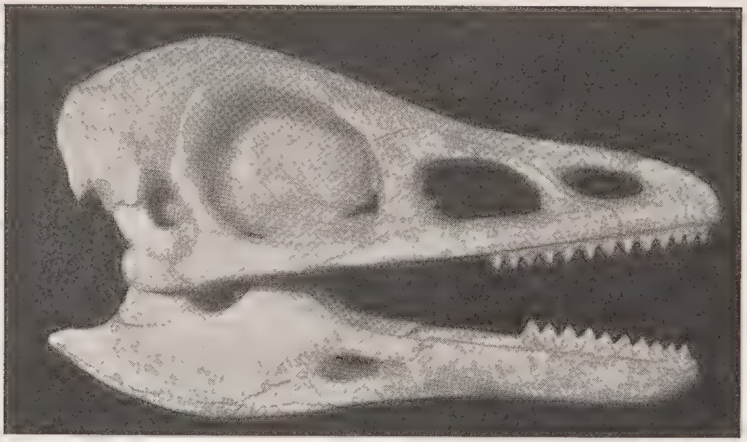


Fig. 1. *Modell des Schädels von Archaeornis.* Ansicht von der Seite. Grösse des Modells: von der höchsten Stelle des Hinterhauptes bis zur Schnabelspitze: 27 cm. (= Das 5-fache des Originals.)

Knochenteile dann noch durch verschiedene möglichst kontrastreiche Farben gegeneinander abgegrenzt. Schon hierdurch wurde eine viel klarere Vorstellung über die Plastik des Schädels und das Verhältnis der einzelnen Knochenteile zueinander erzielt, was sich dann noch zusätzlich durch vorsichtiges Eintragen von Schattierungen verstärken liess.

Auf diese Weise wurde zunächst durch eine mehrfach wiederholte zeichnerische Arbeit auf dem Reissbrett eine Vorstellung über die mutmassliche Lagerung des Vomer und einzelne Teile des Palatinum, wie vor allem auch des Quadratum, gewonnen. Diese an der Seitenansicht erarbeiteten Vorstellungen wurden dann durch Umzeichnen auf Ansichten von oben (nach Heilman), unten, von vorn und rückwärts auf die tatsächlich räumliche Anordnungsmöglichkeit überprüft.

Bei dieser, wie gesagt, rein konstruktiven Arbeit auf dem Reissbrett wurden ferner Angaben über die Schädel von *Campsognathus* (nach v. Huene, Heilman) und dem theoretischen *Proavis* von Heilman berücksichtigt, ebenso in weitgehendem Masse die entsprechenden Verhältnisse bei den rezenten Sauropsiden insgesamt. Massgebend waren dabei aber immer die sichtbaren Konturen der fraglichen Knochenteile der Gaumenplatte. Im Grunde galt es dabei gewissermassen nur die Linienführung dieser Knochenteile, die durch aufliegende Knochen verdeckt sind, sinngemäss weiterzuführen.

Auf diese Weise wurde schliesslich mit einiger Sicherheit Vomer, Palatinum und Quadratum formmässig ermittelt. Einzig allein das Pterygoid musste dann in die Lücke zwischen Palatinum und Quadratum ohne jede

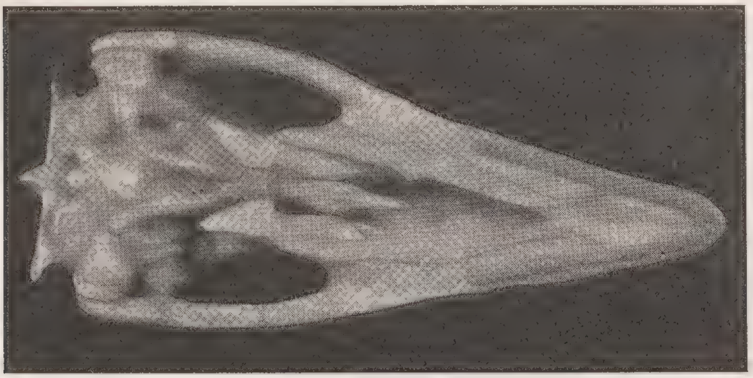


Fig. 2. Ansicht des Schädel-Modells von unten.

Hilfe hineinkonstruiert werden, da es praktisch am Schädel selbst nicht sichtbar ist. Die am Modell ausgeführte Form dieses Knochens kann daher keinen Anspruch auf tatsächliches Verhalten erheben.

Im ganzen ergab sich für den Kiefer-Gaumen-Apparat eine reine schizognathe Form. Der spitze Vomer umfasst das Rostrum, ebenso die lamellenförmigen medialen Platten des Palatinum, das sich seitlich mit dem ebenfalls lamellenartig — wahrscheinlich — sich darüberschiebenden Proc. pal. maxillae verbindet. Für das theoretische Pterygoid wurde Form und Artikulation ähnlich wie bei den Columbidae, Anseres, Charadriidae und Phasianidae angenommen, bei denen dasselbe in einem besonderen Gelenk mit dem Parasphenoid artikuliert, da dieses offensichtlich als primitives Merkmal angesehen werden kann.

Grosse Schwierigkeiten bereitete es, eine einigermassen glaubhafte und logische Form für die einzelnen Lamellen des Palatinum zu finden. Um diesem Problem gerecht zu werden, wurde wieder auf konstruktivem Wege durch sorgfältiges Eliminieren ein paramedianer Aufriss des Schädels von der Seite entworfen. Hierbei wurde gewissermassen die eine Seitenwand „abgetragen" („schichtweise fortgedacht") und entsprechend die „freigelegten" Teile durch Fortführen der ursprünglich sichtbaren Konturen ergänzt und nachgezeichnet. Es ist verblüffend, mit welchem Grad von Sicherheit sich dabei zwingend gewisse Formen, die bis dahin von anderen Knochenteilen verdeckt wurden, gewinnen lassen. Auf diese Weise wurden Beziehungen des Vomers zum Palatinum und zum Rostrum des Ethmoidale festgelegt, ferner aber mit verhältnismässig grosser und verblüffender Sicherheit die Form des Quadratum (Fig. 3). So konnte z. B. ganz leicht der Endpunkt bezw. die verdeckte Spitze des Proc. muscularis bestimmt

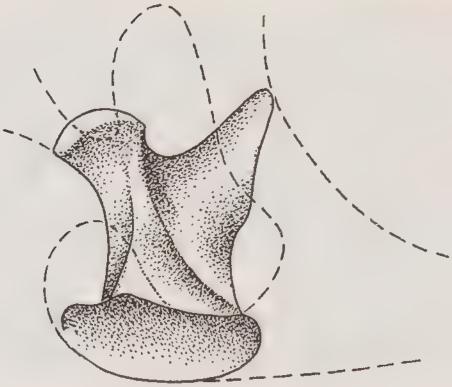


Fig. 3. Rechtes Quatratum. Seitliche Ansicht.

werden. Ebenso ergeben sich bei entsprechender rechtwinkliger Gegenüberstellung der Zeichnungen von Seitenansicht und Aufsicht des Gesamtschädels zwangsläufig die Artikulationsachsen des Quadratum mit dem Schädel. Mit dem gleichen hohen Wahrscheinlichkeitsgrad liess sich Form, Art und Weise sowie annähernde Flächengrösse der Adhäsionsfläche des Quadratum mit dem occipitalen Jochbogenfortsatz, dem Quadratojugale, feststellen.

Durch die gleiche Methode, der rechtwinklig angeordneten und sich überschneidenden Zeichnungen, wurde die Grösse des Gehirnschädels ermittelt, und zwar sowohl von der Seite wie von oben. Auch hier konnte durch verhältnismässig wenig Anhaltspunkte das Wesentliche ohne weiteres ermittelt werden. Zur Kontrolle wurden hier gleiche Rekonstruktionen an Skizzen rezenter Vogelschädel vorgenommen, so dass exakte Vergleiche für annähernden Gehirnumfang in Seitenansicht und Aufsicht möglich sind.

Nach Durchführung dieses soeben geschilderten Konstruktionsverfahrens wurden Ansichten des Schädels von sämtlichen Seiten gefertigt, wieder durch Anwendung des Systems sich rechtwinklig überschneidender Hilfslinien, wobei sich noch geringfügige notwendige Rektifizierungen ergaben. Es wurde dabei besonderer Wert auf das einwandfreie Übereinstimmen der einzelnen Schädelknochengrenzen gelegt, wodurch sich eine grössere Sicherheit für die Beurteilung der tatsächlich plastischen Form ergibt. Das Quadratum wurde hierbei gesondert durchgearbeitet. Erst dann wurden diese linearen Zeichnungen in plastische umgearbeitet und schliesslich Werkzeichnungen angefertigt. Nach diesen konnte dann ein erfahrener Präparator an die Herstellung des plastischen Modells gehen (Fig. 1, u. 2). Bei der Ausführung dieses Modells wurden aber ständig die rein zeichnerisch gewonnenen Vorstellungen überprüft, ob sie sich auch praktisch logisch und in einwandfreier Form verwirklichen liessen. Wir konnten mit Genugtuung feststellen, dass in dieser Hinsicht nur ganz minimale Änderungen notwendig waren.

Die Occipitalfläche des Schädels habe ich weitgehend unbeachtet gelassen, da hier nur sehr wenig Anhaltspunkte für die Ausformung im einzelnen zu gewinnen sind.

Der Unterkiefer stellte im grossen und ganzen weder konstruktiv noch formmässig irgend welche wesentlichen Probleme bis auf die Gestaltung des Gelenks, dessen Fläche ebenso wie bei dem entsprechenden des Quadratum stark theoretischen Charakter tragen musste.

Für die museale Darstellung wurde zum besseren Verständnis in gleicher Grösse (fünffach) ein Taubenschädel gefertigt, der nun mit dem daneben gestellten Originalschädel eine gute Vorstellung der tatsächlichen Grösse des Archaeornis-schädels und seiner wesentlichen Merkmale dem Beschauer vermittelt. Für gleiche Zwecke wurde im übrigen ebenfalls in fünffacher Vergrösserung nach den verschiedenen Angaben die Becken der beiden Urvögel plastisch dargestellt, wobei auch die jüngsten Angaben von M. Friant (1948) beachtet wurden. Durch weitere plastische Modelle, besonders einer Gesamtrekonstruktion des lebenden Archaeornis, ferner einer entsprechenden Plastik des theoretischen Proavis nach Heilman und weiteren Rekonstruktionen von Compsognathus, Podokesaurus und Ornitosuchus sowie Darstellung vergleichsanatomischer Tatsachen und Beziehungen zu rezenten Primitivismen bei einzelnen Vögeln und Echsen haben wir so in der Schausammlung des Naturhistorischen Museums in Braunschweig versucht, eine Darstellung über das Problem der Genese des Vogelstammes zu geben.

## Literaturverzeichnis

Dames, W., 1884. Über Archaeopteryx, Palaeontol. Abhandl. II.

— — 1896. Über Brustbein, Schulter- u. Beckengürtel der Archaeopteryx. Sitzber. d. preuss. Akad. d. Wiss.

Friant, M., 1948. Sur la morphologie de l'os pubis chez les oiseaux. Compt. r. Akad. Sc. 226.

Heilman, G., 1926. The Origin of birds. London.

Owen, R., 1863. On the Archaeopteryx of von Meyer with Description of a long-tailed species from the Lithographic stone of Solenhofen. Philosoph. Transact. Roy Soc. London CLIII.

# Growth and Differentiation of the Brain in Nidifugous and Nidicolous Birds

*Ernst Sutter*

*Museum of Natural History, Basle*

In studying the postembryonic development of birds we meet with such extreme contrasts as the active chick of the Galliformes and the helpless nestling of the Passeriformes. Field ornithology has done much work in this domain of bird biology, but the comparative morphology of the different types of ontogenesis is still at the beginning. Portmann (1935) has made an attempt in this line, and since some more work has been performed under his direction at the Zoological Institute of the University of Basle, endeavouring a detailed quantitative and morphological analysis of the avian ontogenesis. Some of the results of the investigations of the central nervous system made by Portmann (1942, 1946–47), Kocher (1948), Schifferli (1945, 1948) and the author (1943, 1946) will be reported here.

We shall examine first the situation on the hatching day. Comparing the nidifugous chick of *Megapodius* (Galli) with the nestling of *Turdus* (Passeres) we find the brain development of the former much more advanced (Fig. 1). The brain weight of the newly hatched *Megapodius*[1] amounts already to 40 % of the adult weight, and the proportions of the parts of its brain too reach almost the state of maturity. The degree of brain development fits the independence of the chick, which from hatching grows up without any care of its parents.

On the other hand the nestling of *Turdus,* hatching blind, naked and depending entirely on its parents, has a much smaller brain. The brain weighs scarcely 10 % of the adult weight, and its proportions are quite embryonic: the hemispheres and the cerebellum with 6–7 % of the adult weight are fare behind the corpora bigemina (26 %) and the stem remnant (21 %). The immature state of the nidicolous nestling might likely be attributed to the shorter incubation period, but in fact it is correlated with the particular

---

[1] Material collected by the Sumba-Expedition of the Museum of Natural History Basle.

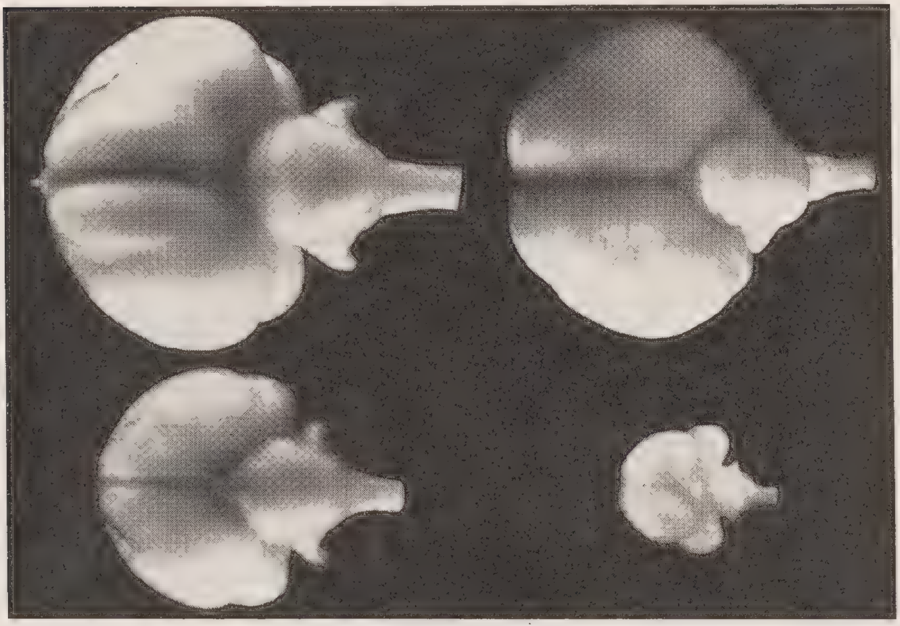


Fig. 1. Adult and hatching brain of *Megapodius freycinet* (left) and *Turdus merula* (right). (Adult and young at the same scale.)

circumstances of the postembryonic growth in this group of birds. This will be pointed out in considering the growth of the whole body.

We see in fig. 2 that species of similar size have the same hatching weight, irrespective of the duration of the incubation period (e. g. *Coturnix* 17 days, *Sturnus* 13 days). Considering the relation of brain weight to body weight, it is evident how much the brain dominates in young gallinaceous birds, rails and waders. The growth of the brain is very much advanced compared with other organs. The hatching brain of *Coturnix* e.g. has only to increase its weight 3 times to reach adult size, while the body weight increases as much as 21 times. Thus the brain amounts to 5–7% of the body weight in the chicks and only to 0.2–0.9 % in the mature gallinaceous birds.

In nidicolous birds the brain is not only absolutely but also in relation to the body weight much less developed. At first sight this may appear strange. Considering that the brain of the adults outweighs that of gallinaceous birds of similar body weight 2 or 4 times, one might expect this superiority to be present in the nestling already. Further it is a rule that the relative brain weight is the highest in the early embryo, and decreases continuously during

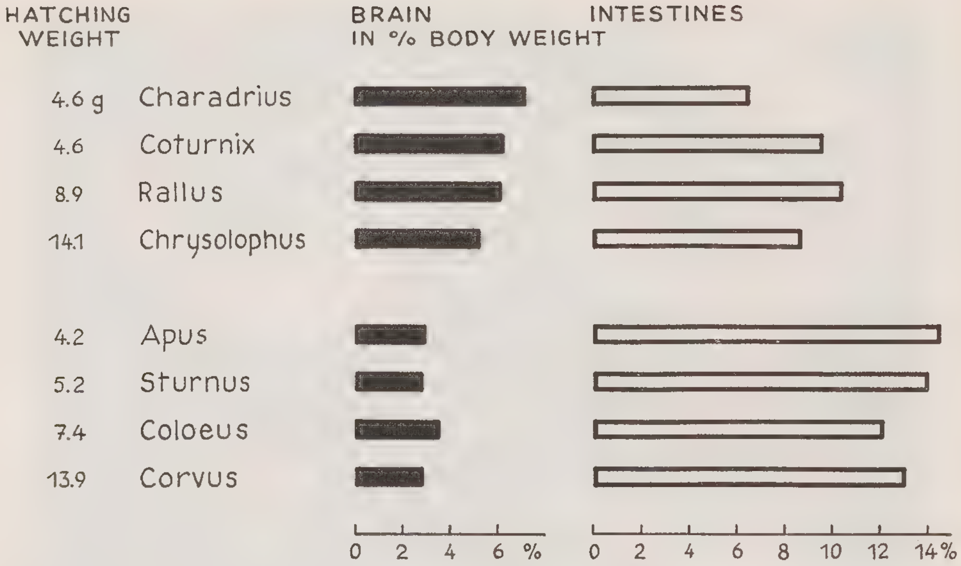


Fig. 2. Relative weight of brain and intestines in nidifugous (above) and nidicolous (below) hatchlings.

its development. Now we find in the nidicolous hatchling, whose central nervous system offers in many regards quite embryonic features, a smaller brain than in the more advanced nidifugous chick. The ponderal analysis of the other organs, however, shows that the organs of metabolism are particularly well developed, as is demonstrated in fig. 2 with regard to the intestines. The relatively heavy weight of these organs stands in direct correlation with the very intensive postembryonic growth so characteristic of the nidicolous birds. With relation to the brain this means that the embryonic growth of this organ is retarded in favour of the alimentary system. So the nidicolous bird differs greatly from the nidifugous, whose brain growth is rather accelerated during the embryonic period with regard to its active mode of life after hatching. This might be pointed out in detail in discussing the graphs fig. 3.

In studying the ponderal growth we determined the fresh weight and the dry weight of the brain dissected into its four major parts: the hemispheres, the corpora bigemina, the cerebellum and the stem remnant[1], the latter containing the medulla oblongata, the basal part of the mesencephalon and the diencephalon.

[1] This term may be introduced for the "Stammrest" of our publications.

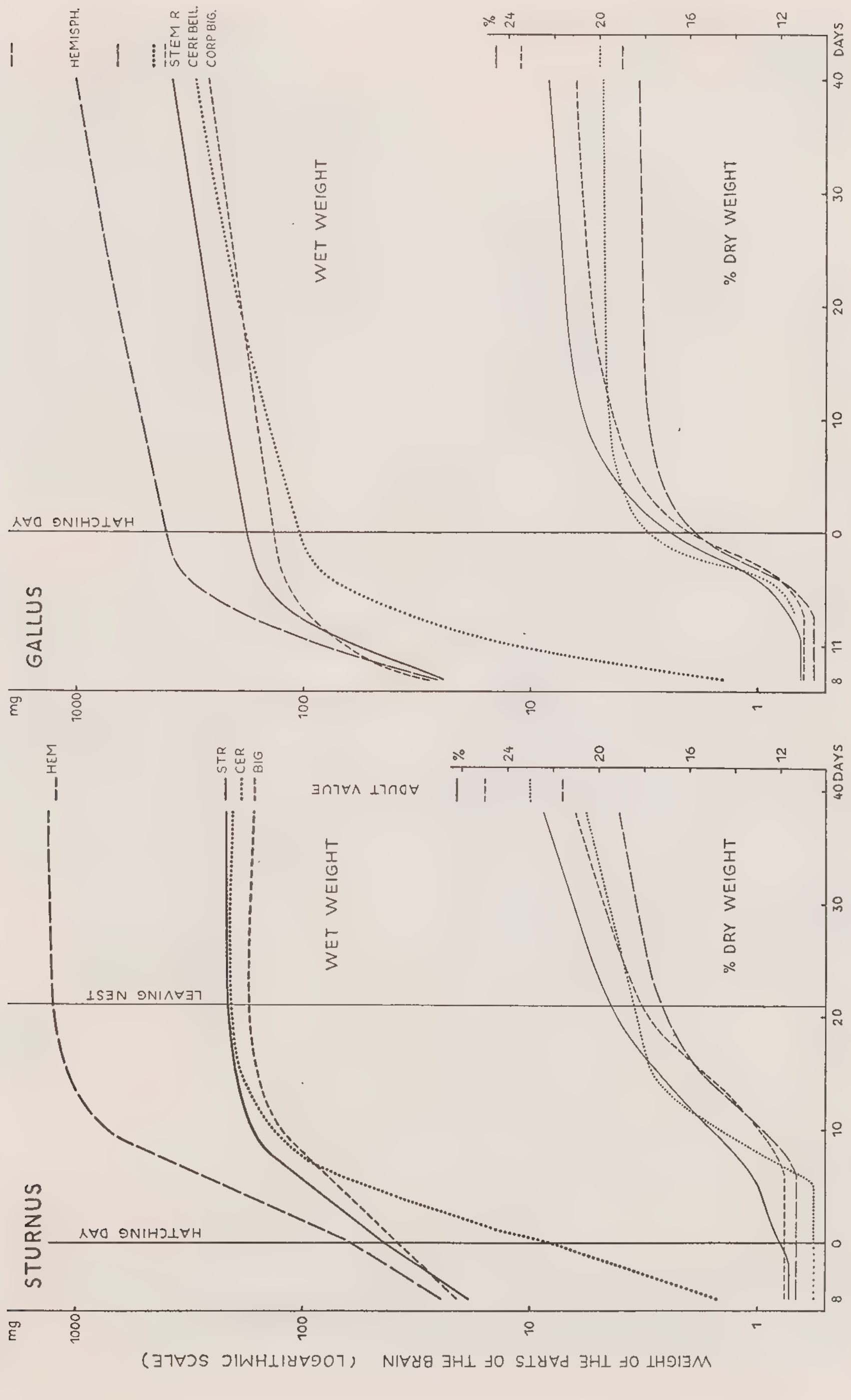


Fig. 3. Explanation in text.

The growth type of the nidifugous bird is represented by the graph of the chick (Gallus). All parts of the brain increase at the beginning very rapidly. Approaching the hatching the growth rate decreases continuously and passes over to the very slow rate of the postembryonic growth. The final weight is not reached till the age of 9 months. The relative increase of the solids gives us further insight into the growth process. The percentage of dry substance is at its smallest in the undifferentiated embryonic tissue and reaches its maximum in the mature oblongata, which is particularly rich in myelinated fibres. Its increase is in close relation to myelinisation (Schifferli 1948, Sutter 1943), and gives a useful measure of the degree of the histological differentiation. Beginning with the oblongata the percentage of dry substance rises rapidly from the 15th day of incubation and reaches a high value already at hatching out. This statement agrees well with the observations of Schifferli that the myelinisation is far advanced at this time. Everywhere from the oblongata to the diencephalon, and in the basal parts of the hemispheres we find a dense network of myelinated fibres. Thus the nidifugous bird develops toward the hatching moment a brain which in relation to the body weight is very large, and which in the proportions of its parts as well as in its histological differentiation comes very near the state of maturity.

In the Starling (*Sturnus vulgaris*) the embryonic growth proceeds somewhat slower and is much less productive than in the chicken. After hatching it is exactly the contrary. A slower growth rate, being elsewhere the rule, is found only in the stem remnant. The other parts grow for another week at an unchanged, and the hemispheres even at a considerably higher rate. They reach their final size in an astonishing short time. For a while the wet weight even surpasses the adult value, which is to be attributed to the higher water content of the juvenile brain.

The percentage of dry substance remains for a long time on the embryonic level, which indicates that the process of differentiation begins relatively late. This is one of the most important peculiarities of the nidicolous type of development. Such an extraordinary rapid growth, as in this first postembryonic week, seems to be only possible as long as the tissue remains in a relatively undifferentiated state. The histological maturation does not go on till the ponderal growth is nearly finished. This way of development is closely related to the particular circumstances in which the nidicolous bird grows up. The whole development from hatching to adult size proceeds under the protection of nest life. Therefore the full functions of the brain are not needed before the young leaves the nest. Further on we may see in the dissociation between ponderal growth and differentiation

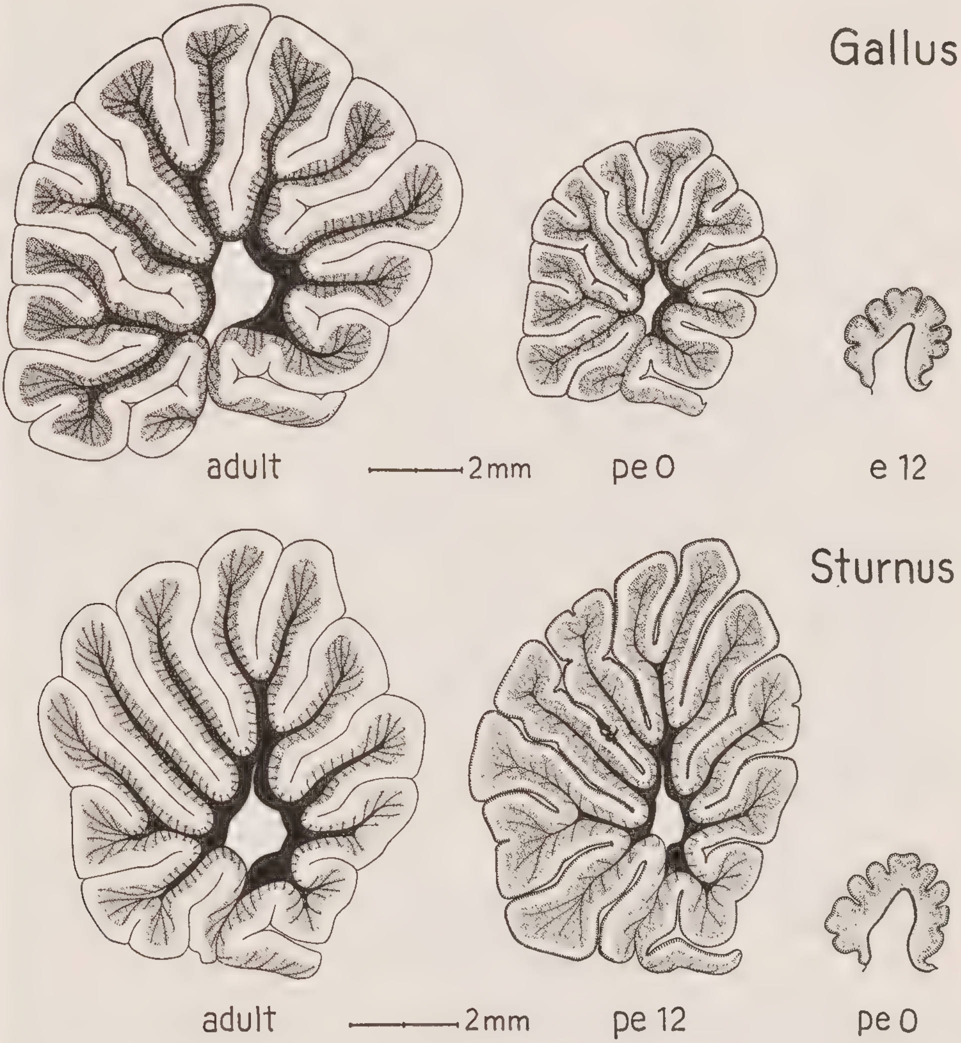


Fig. 4. Midsagittal sections of the cerebellum of *Gallus domesticus* and *Sturnus vulgaris*.

Molecular layer white, granular layer dotted, myelinated fibres black, embryonic superficial cortex hatched. Pe = postembryonic day, pe O = hatching day, e = embryonic day.

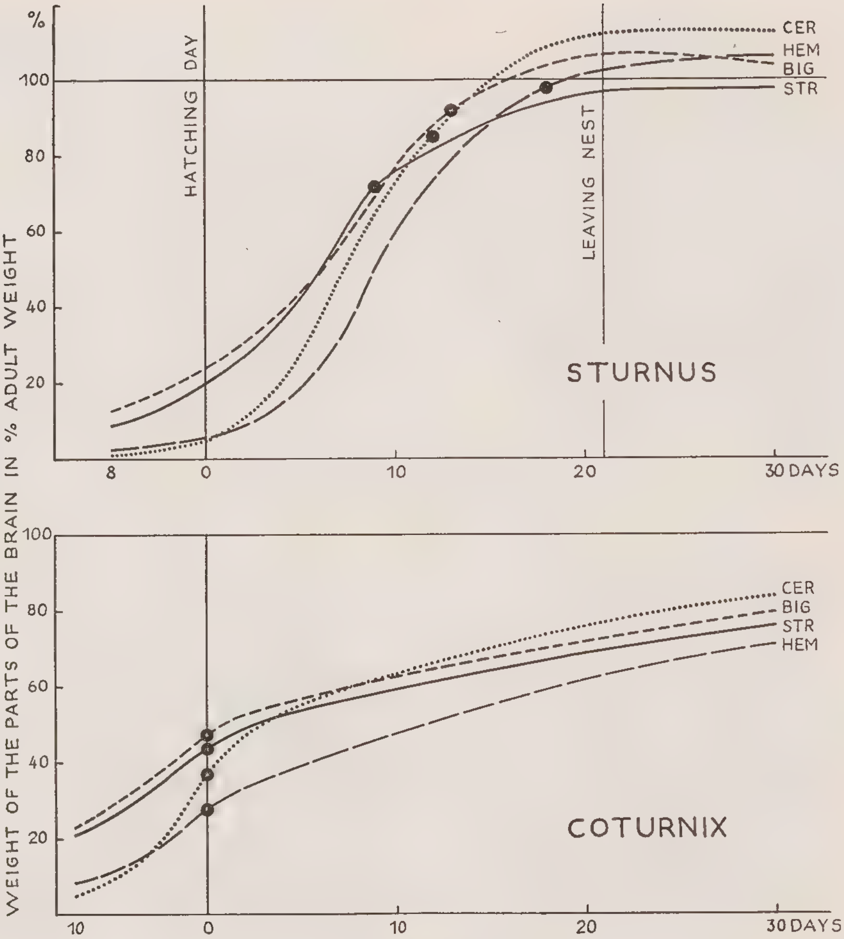


Fig. 5. Explanation in text.

the possibility to push on the development more rapidly, in order to shorten the nestling period.

Our discussion of the graphs may be completed by regarding different phases of the histological development of the cerebellum represented schematically in fig. 4. The cerebellum of the hatching Starling (incubation period 13 days) corresponds to that of a 12 day old chick embryo. Myelinated fibres are not yet formed. In the newly hatched chick (incubation period 21 days) we find a cerebellum, which does not differ essentially from the adult one, except for the myelinated fibres growing somewhat closer and stronger, and the molecular layer being enlarged subsequently. When it arrives at the highly differentiated hatching state it weighs not more than 24% of the adult cerebellum. The nestling of *Sturnus* does not reach an adequate point of myelinisation till at the age of 12 days. At this time its cerebellum amounts already to 85% of the adult weight, which shows clearly the different relation between relative size and degree of myelinisation mentioned above.

The growth analysis and the investigation of the histological development are combined graphically in fig. 5. The solid dots in this graph indicate the degree of myelinisation reached in the hatching Quail (*Coturnix coturnix*). We see that in the nidicolous group, represented by *Sturnus*, the various parts of the brain reach that state of myelinisation at different times. This fact proves again the fundamental difference between the two types of development. With relation to *Sturnus* it is interesting to note that the brainstem, in which the basic brain functions are located, precedes the other parts, while the differentiation of the hemispheres is delayed. The latter reach in the mature organ the highest complication, and become much larger than those of the gallinaceous birds. This implies a longer period of development. Moreover the graph shows the different aim of development in either of the two groups. In the nidifugous type an early efficiency of the brain is needed and therefore the essential processes of growth and differentiation are chiefly performed during the embryonic life. After hatching the brain grows very slowly according to its advanced state of differentiation. In the nidicolous type the main growth takes place in the postembryonic period, and the full functional efficiency of the brain is reached almost together with the completion of the ponderal growth.

After having considered some development problems in birds we might shortly discuss the evolutional significance of the different ways of ontogenetic development. According to Portmann (1942, 1946–47) the type of ontogenesis is closely related with the degree of cerebralisation. The nidifugous birds represent the families with the relatively smallest brains, while all high cerebralised birds belong to the nidicolous group. It seems that only birds with a comparatively small brain can realise at hatching that advanced degree of brain differentiation, which already matches functionally the adult state, as it is the case in the nidifugous forms. From this we may conclude that in the nidifugous type the relative brain size is limited. If this hypothesis is right, the nidicolous way of development appears to have been a fundamental phylogenetic step enabling further progress in the cerebral evolution of the birds.

## References

KOCHER, C., 1948. Das Wachstum des Gehirns beim Alpensegler. (*Micropus m. melba* L.). Rev. Suisse Zool. 55: 57–116.

PORTMANN, A., 1935. Die Ontogenese der Vögel als Evolutionsproblem. Acta biother. 1: 59–90.

—— 1938. Beiträge zur Kenntnis der postembryonalen Entwicklung der Vögel. Rev. Suisse Zool. 45: 273–348.

—— 1942. Die Ontogenese und das Problem der morphologischen Wertigkeit. Rev. Suisse Zool. 49: 169–185.

—— 1946–47. Études sur la cérébralisation chez les oiseaux. I–III. Alauda 14: 2–20, 15: 2–15, 161–171.

SCHIFFERLI, A., 1945. Vergleichende Untersuchungen über den cerebralen Myelinisationsprozess bei Huhn und Star. Rev. Suisse Zool. 52: 377–382.

—— 1948. Ueber Markscheidenbildung im Gehirn von Huhn und Star. Rev. Suisse Zool. 55: 117–212.

SUTTER, E., 1943. Über das embryonale und postembryonale Hirnwachstum bei Hühnern und Sperlingsvögeln. Denkschr. Schweiz. Nat. Ges. 75, Abh. 1: 1–110.

—— 1946. Über das Wachstum des Kleinhirns bei Vögeln. Rev. Suisse Zool. 54: 447–454.

# The Structures in the Avian Pituitary Responsible for the Transfer of Impulses from the Nervous to the Hormonal System

*K. G. Wingstrand*

*Zoological Institute, Lund*

A detailed examination of the pituitary region of birds reveals a distinct tractus hypophyseus which, mainly at least, arises from the hypothalamic nuclei. The fibres thereupon run downwards to the eminentia mediana, where they form the tract. Finally they enter the neural lobe and form a dense tangle throughout this organ. The secretory activity of the neurohypophysis (including the eminentia, neural lobe and infundibular stem) may thus be directly controlled via this tractus. The pars distalis (an intermedia is completely absent) has not been found to contain any distinct nervous elements, but the possibility of a nervous system there with peculiar staining properties cannot be definitely rejected. Apart from the possibility of a nervous control in this way, the gland may be controlled in a humoral way by a system of portal vessels. This system is supplied by infundibular arteries from the carotis cerebralis. The first capillary net covers the surface of the eminentia mediana. From here the blood is transported to the sinusoid capillaries of the pars distalis by a few large portal vessels, which are embedded in the pars tuberalis. The pars distalis does not receive any direct arteries and is drained directly into the surrounding "sinus cavernosus". Now the superficial layer of the eminentia is in intimate contact with the primary capillary net, and, moreover, presents a structure which strongly suggests a secretory activity. The substances secreted must necessarily be transported to the pars distalis. If these substances influence the secretory activity of this gland, there will be a neuro-humoral control of the gland similar to that suggested by Harris and Green in particular for a number of other animals. Thus there will be a nerve conduction from the hypothalamic nuclei to the eminentia and a humoral transfer of the stimuli from the eminentia to the pars distalis. The aim of the present investigation was to find the structural bases for a transfer of stimuli from the hypothalamus to the pituitary—the choice among the possibilities indicated must be made by physiological experiments.

A more complete account will appear in a future paper.

*Discussion:*

H. Giersberg: Die Annahme einer humoralen Übertragung der Stimuli von der Pars neuralis zum Vorderlappen gibt eine mögliche Lösung der Frage der Art der Hypophysenregulation, die bisher auch för den Menschen noch nicht genögend geklärt ist.

G. J. van Oordt asks whether it might be concluded from Dr. Wingstrand's observations that the thyroid hormone and oestrogenic hormone act directly, through bloodvessels, on the pars distalis.

K. G. Wingstrand: I think there are two possibilities, one is the direct influence of the hormone on the cells of the pars distalis. The other is that the cells of the hypothalamus become irritated by the hormone, and these impulses are transported to the pars distalis in the way just indicated.

# Das Flugvermögen der seglerartigen Vögel (Macropterygidae)

*Adolf Kleinschmidt*

*Naturhist. Museum, Braunschweig*

Das Streckungs-Verhältnis (der Längen-Breiten-Index) des Flügels der seglerartigen Vögel (Macropterygidae) liegt mit dem der echten Segelflieger (Longipennes) im wesentlichen auf gleicher Höhe. Mit gewissen Einschränkungen trifft dies auch für den Gesamtlängen-Flügellängen-Index zu. Die aerodynamische Leistungsfähigkeit der Flügel und mithin das Flugvermögen der Macropterygidae ist daher trotz grundlegender Verschiedenheit im proportionalen inneren anatomischen Aufbau wie der Proportionen der äusseren Schwingen-Ausstattung, nicht zuletzt auch der Flugform, effektiv dem der Longipennes gleich.

Bei weitaus der Mehrzahl der Formen lässt sich ferner ein deutliches Nord-Süd-Gefälle mit Verschlechterung der Werte nach Süden zu für das Streckungs-Verhältnis der Flügel nachweisen. Obschon bei den Seglern die nordischen Formen echte Zugvögel sind, dürfen für ein derartiges Vorhandensein der günstigeren aerodynamischen Flügelform in nördlichen Gebieten selektionistische Momente nicht *die* Rolle spielen, wie bei weniger fluggewandten Vögeln, da die Macropterygidae an sich schon ausgesprochene Dauerflieger sind.

(Die ausführliche Darstellung erscheint in "Syllegomena biologica" Festschrift für Otto Kleinschmidt, Wittenberg/Lutherstadt, zu dessen 80. Geburtstag am 13.12.50.—Gemeinschafts-Verlag: Akad. Verlagsges. Geest & Portig K. G. Leipzig — A. Ziemsen Verlag, Wittenberg/Lutherstadt.)

# Researches of the Severn Wildfowl Trust

*Peter Scott*

*Severn Wildfowl Trust, Slimbridge, England*

For ducks, geese and swans, the struggle for existence against the spread of civilisation becomes increasingly difficult. In nearly all parts of the world further steps are necessary if the stocks are to be maintained and if a number of species are to be saved from extinction. In order to know what these steps should be much study and research is still needed into the biology of this group of birds, and at the same time it is desirable to encourage public interest in the subject.

For these purposes a Research station and Observatory was set up in 1947 on the west side of England at the mouth of the River Severn. This organisation is known as the Severn Wildfowl Trust. It is working in cooperation with the International Wildfowl Research Institute at Tring and the Observatory and Ringing Schemes of the British Trust for Ornithology. Within the limits of this paper there is not space to give more than a brief description of the station and to list the principle studies which are now being undertaken by the Trust and by visiting students.

The sand banks and mudflates of the Severn Estuary are bounded on the south side by a grass salt marsh which is the principal winter feeding ground of a large flock of wild geese. This flock, sometimes 4 000 strong, consists mainly of White-fronted Geese (*Anser albifrons albifrons*). There are also, especially in the early part of the winter, small numbers of Pinkfooted Geese (*Anser fabalis brachyrhynchus*). Besides these two species all 13 of the forms of geese on the British List have been recorded including 9 of the 12 British records of the Lesser Whitefronted Goose (*Anser erythropus*). These records indicate that this species is a regular visitor to Britain in very small numbers and had previously been overlooked. The occurrence of this and other species of geese usually as single birds in the flocks of *A. a. albifrons* affords an interesting example of aberrant migration which is not unusual among geese.

By means of a series of specially constructed observation huts overlooking the feeding grounds, which can be approached from behind a sea wall, it has been possible to study the geese at close quarters. This has yielded statistics on the breeding success of *A. a. albifrons*. Behaviour studies have been undertaken, notably those connected with the social structure of the flocks, and with "peck-order."

The geese have been caught here (and also in other parts of Britain) by means of rocket-propelled nets in order to ring them, and to mark them with dyes. Experiments to find the most lasting kinds of dyes continue. During the past winter 71 geese were caught at one discharge of two nets. The catch for the season was 69 Whitefronted Geese, 7 Pinkfooted Geese and 29 Greylag Geese (*A. a. anser*), a total of 105. Now that the technique has improved much greater catches are expected.[1]

The main feeding ground of the geese lies about 300 yards from the group of cottages which form the Headquarters of the Trust. Between these two, and surrounded by a small wood, is the Duck Decoy. This was built just over 100 years ago and has four pipes. It is now used exclusively for marking and about 1 000 ducks of 8 species (*A. platyrhynchos, A. crecca, A. clypeata, A. acuta, A. penelope, A. querquedula, A. strepara, A. fuligula*) have been ringed and released. Observation huts have been constructed on the edge of the decoy pool in order that the ducks may be studied closely.

In some 20 acres of low lying fields which surround the decoy are a number of enclosures in which special ponds and ditches have been dug. About 700 ducks, geese and swans of 120 forms live in these enclosures.

These afford excellent opportunity for systematic comparison. Shape, carriage, voice, colour of soft parts, behaviour and many other aspects, which can only be shown by the living bird, all add to our knowledge of the evolution of the Anatidae. In the field of ethology a number of special studies have been undertaken, notably on preening, nuptial display and imprinting. Many of the experiments have been made at the suggestion of Dr. K. Lorenz when he visited the station.

The Trust has been active in support of particular species which are threatened with extinction. Early in 1950 J. Yealland, Curator of the Trust's collection, was invited to go to Hawaii to advise the Board of Agriculture of the Territory of Hawaii upon the propagation of the Ne-ne or Hawaiian Goose (*Branta sandvicensis*). Only 5 wild birds have been seen recently, although it is just possible that up to 20 exist. There are a further 19 in captivity. Yealland was successful in raising 2 young birds from the only 2 fertile eggs laid by the captive birds. He also brought to Europe a pair of 4 year old geese and it is hoped that a breeding stock can be established on the Seven Estuary. Meanwhile the world stock of this fine bird stands at between 24 and 40 individuals.

---

[1] In the 1950–1951 season 734 geese (mostly Pinkfooted) were caught with rocket nets for ringing.

The Koloa or Hawaiian Duck (*Anas wyvilliana*) is also represented in the Trust's collection. The species is between 300 and 500 strong and appears still to be declining. A European breeding stock is therefore very desirable. Another island species which may be threatened is the Philippine Duck (*Anas luzonica*) which is represented by a well mated pair on the Severn Estuary.

Some 50 species and subspecies of Anatidae have nested in the enclosures and a large number of young birds has been reared, mostly under hens and bantams as foster parents. When the first clutch is removed for incubation a second, and sometimes even a third, is laid. The renesting interval in captivity has been shown to be several days longer than that met with in the wild state (Sowls 1950).

Full results of the Trust's work appear in a Report published annually. (These Reports may be obtained from the Secretary, the Severn Wildfowl Trust, Slimbridge Gloucestershire, England).

The Trust's Research Station is available for any student wishing to carry out a study of the Anatidae and delegates to the Congress are cordially invited to pay a visit to the Severn Estuary whenever they may be able so to do.

The colour film which accompanied this paper included shots of the following subjects:—Whitefronted Geese (*A. a. albifrons*) feeding on the grass salt marsh at ranges down to 8 yards. Among them one Pinkfooted Goose (*A. a. brachyrhynchus*), one Greylag Goose (*A. a. anser*), Shelducks (*Tadorna tadorna*), Starlings (*Sturnus vulgaris*), and Curlews (*Numenius arquata*). Rocket nets being fired and the capture of 71 geese at one discharge, as well as subsequent catches of Greylags, showing the ringing of the birds and spraying with dye. The working of the Duck Decoy including the use of the Decoy dog which attracts the ducks into the pipe, and the subsequent ringing and release of the captured ducks. Also the courtship display of the European Greenwinged Teal (*Anas c. crecca*).

The film included a number of general views of the collection of live waterfowl followed by individual shots (not in the order of classification) in which among others the following were seen:—Puna Teal (*Anas versicolor puna*) male preening on shore; Philippine Duck (*Anas luzonica*) pair; Ruddy Duck (*Oxyura jamaicensis*) in winter plumage diving, and in summer plumage male displaying to female; Radjah Shelduck (*Tadorna radjah*) female; Greater Snow

Goose (*Anser hyperboreus atlanticus*) and Emperor Goose (*Anser canagicus*) feeding from hand; Ne-ne or Hawaiian Goose (*Branta sandvicensis*) pair; Redbreasted Goose (*Branta ruficollis*); Greylag Goose (*Anser anser anser*) in flight, sitting on nest and washing, also in comparison with the Eastern Greylag Goose (*Anser anser rubrirostris*); Cape Barren Goose (*Cereopsis novae-hollaendiae*) pair with downy goslings; Blue Goose (*Anser caerulescens*) male defending kennel-type nesting box to which it has been mated for two seasons (during spring and summer only); Perry River Whitefronted Goose (*Anser albifrons s. sp.*) male showing aggressive behaviour when handled; Ross's Goose (*Anser rossii*) group brought back from Perry River region of Northern Canada; Goosander (*Mergus merganser merganser*), male, walking on slippery ice. A sequence was devoted to a visit by H. R. H. Princess Elizabeth and another showed how large numbers of visitors could wander among the birds without causing disturbance.

## Reference

SCOTT P., 1949. Key to the Wildfowl of the World. Published by the Severn Wildfowl Trust.

# Conservation on Ornithological Programs

*Grace E. Barstow Murphy*

*New York*

During several decades of attendance at the Annual Meetings of the American Ornithologists' Union, I have watched on the programs the developing relationship between Conservation and Ornithology. I have studied various indexes with the constant thought that the past is the foundation which affects the present and that the present with its widened attainments points to the all-important future.

At the First International Ornithological Congress held in Vienna in 1884, a project for an International Law to Protect Birds was made. It has developed into the three-day meeting held in Upsala, preceding the opening of this Tenth Congress. Last week papers on Conservation were presented, the main program of the Congress being reserved for ornithology, as has been the custom of the intervening congresses.

It is not possible to cover in a few moments the programs of even all our American ornithological associations. I will consider only three of these, which represent our whole country.

The Cooper Ornithological Club of the western United States in its Bulletin "The Condor" carries no titles on Conservation. Its titles relate to the pure science of ornithology. This is also true of the British Ornithologists' Union in the "Ibis." Both these organizations stand strongly for Conservation.

The Wilson Ornithological Club, centred in our middle states yet with a countrywide membership, states in Section 2, Article 1, of its Constitution: "The object of the Wilson Ornithological Club shall be to advance the science of ornithology." Later this is interpreted as being fundamental to bird Conservation, and it is stated "hence the position in that field is clear-cut." Resolutions backing conservational needs are frequently made at meetings. In 1931, Dr. T. G. Pearson's paper before this club on "The Conservation Program of the National Association of Audubon Societies" seems to be the first definite presentation of the subject. The 1932 and 1934 programs are peppered with pleas against the slaughter of hawks and owls. In 1935 Roger Petersen gave a paper on "Building Conservation for the Future," and in 1936 William Vogt spoke on "A Rational Basis for Conservation." In the early forties, the title: "Wildlife Conservation" took its place in the Table of Contents of the Bulletin.

The American Ornithologists' Union, founded in 1883, has profoundly affected the study of ornithology in America. Its work resulted in the creation of both the National Audubon Society and the United States Fish and Wildlife Service, formerly known as the Bureau of Biological Survey. The A. O. U. has extended its influence into the fields of legislation and international diplomacy, and has fought the slaughter of birds since 1884. Its publication, "The Auk," which succeeded the Bulletin of the Nuttall Ornithological Club, includes five indexes at ten year intervals.

The first Index, covering the years 1876-1900, has no reference to Conservation, and only two to Bird Protection.

The second Index, covering 1901–1910, has, under The Protection of Birds, seven references.

In the third Index, 1911–1920, there are ten references to the Protection of Birds.

At last, in the fourth Index, 1921–1930, the word Conservation is used, with two references. The Protection of Birds is still listed, with 13 references.

In the fifth Index, 1931–1940, under Protection, the reader is advised to "see Conservation," under which there are 34 references, with a long list under the Committee on Bird Protection. In this fifth Index, the word Ecology is first included, with 34 references.

The idea of Ecology had of course been creeping in from the beginning, even though the name of the new science did not appear on an A. O. U. program till 1930. If we grant that it is the science on which modern techniques of Conservation are built, significance is attached to its early recognitions. For instance at the first A. O. U. Congress in New York in 1883, a Committee on Bird Migration was asked to report on meteorological conditions and the state of advancing vegetation. This general subject of phenology, widely popular at that time, led directly to the rapid development of the more comprehensive science of ecology, evidenced so strongly in our current program.

Yet in 1933, the statement of our distinguished ornithologist Dr. Witmer Stone, is recorded regarding Ecology, "the term is perhaps not so pertinent in ornithology as in botany." Of course birds fly and plants do not, but such flight serves to enhance the interest of their relaton to their environment.

Our Government as far back as 1877 was doing constructive work on the interrelationships of birds and agriculture — work that is increasingly important to a hungry world.

The growth of every branch of ornithology can be traced through titles on the programs. Bicknell in 1884 began his series of papers on "The Singing of our Birds" by saying "no apology is needed," which is a back-handed way of offering apology. The first graphophone demonstrations in our country by Judd in 1898, developing into the work of Aretas Saunders and the recordings of Arthur Allen and the late Albert Brand, present no apology whatever! Similarly, though bird-ringing has been practised over centuries for one reason or another, only to-day do papers based on it deal with such matters as migrations, wanderings, homing, age of birds, dispersal of young. The work has gone so far as to give opportunity to the British for their stroke of genius in interesting the public and raising funds through their duck-adoption plan.

The earlier A. O. U. papers dealt in large part with problems of nomenclature, bird-watching, identification, range, and so on. There were no such studies as "The Adrenal- & Thyroid-Weight in Birds" (Hartman, 1946) or Moore's "Temperature Tolerance of Birds' Feet".

The impact of other branches of science upon ornithology is suggested by the title: "Bird Detection by Radar." The impact of ornithology on other branches of science is suggested by the Symposium on "Birds in the Air" shared with the aeronautical engineers at our 1949 A. O. U. meeting; or such works as by Williers at Johns Hopkins on the effect of sex-hormones on feather pigmentation.

The sixth Index of the Auk is now in course of preparation. What will it list on the vital subject of Conservation? Is the trend of the research ornithologist toward less intellectual isolation in these days when natural history is becoming more and more integrated with many other branches of science?

We have at home many organizations, the publications of which deal primarily with Conservation. The Audubon Magazine, for instance, makes a popular appeal which has far-reaching effect. The Transactions of the North American Wildlife Conference are, on the other hand, technical. Rudolf Bennett, of the University of Missouri, summarized the 1946 Conference, showing that the work was becoming more realistic and less visionary. He stressed that the technical men are obligated to make their work valuable in the world of science and that teamwork must increase and wildlife interests must become international. He said that "we are discussing species, ecological situations and techniques we neither knew nor cared about ten years ago. The advances of two decades have outstripped those of half a century."

Conservation has long passed the stage where arguments as to whether bag limits or refuges provide the most effective protection. Now we know we need both and all we can get of every other constructive method too. Conservation is an art based on science just as medicine is an art based on science, each almost a science in its own right.

The question brought up by this brief survey is: What will be the attitude of the research ornithologist toward Conservation on ornithological programs twenty years from now? With human population increasing and wildlife population decreasing, will the two essential parts of ornithology, research and protection, tend to be accepted as one basic unit? Ornithology cannot even exist as a science, except historically, without the birds that our conservationists preserve. It is particularly appropriate to consider the subject here in Sweden, the country which pointed the way long ago by instituting modern forest management and game protection.

Isolation is a normal human tendency. Research is so absorbing that it is difficult to think outside the subject in hand. Yet it may be a good thing that the recognition of Conservation appears to be growing on our thrilling programs, uniting increasingly the two essential parts of the science which is the very breath of life to each of us in this hall.

# Zur Mitarbeit nichtfachlicher Kräfte in der Ornithologie

*Rudolf Kuhk*

*Vogelwarte Radolfzell (vormals Vogelwarte Rossitten)*
*der Max-Planck-Gesellschaft zur Förderung der Wissenschaften*
*Bodensee*

Es gibt wohl kaum eine andere Wissenschaft, die sich der Anteilnahme und Mitarbeit nichtfachlicher Kräfte in solchem Ausmass erfreut wie die Vogelkunde. Wenn wir zurückblicken auf die Männer, die vor 150 und 100 Jahren den Grundstein zum Gebäude der Avifaunistik, aber auch der Systematik und der Biologie gelegt haben, so wird uns Heutigen vielleicht zu unserm Erstaunen klar, wie wenige dieser ,,Väter der Vogelkunde" mit der Zoologie, ja überhaupt mit der Wissenschaft beruflich verbunden waren. In jener Zeit, als man noch wenig wusste über unsere Vögel und selbst von den einheimischen Arten einige noch gar nicht sicher kannte, als es noch galt, die Lebens- und Ernährungsweise, die Nester und Eier zu beschreiben oder die Lautäusserungen erstmalig kennenzulernen, da konnte jeder, der ein offenes Auge und die Fähigkeit zur getreuen Wiedergabe dessen besass, was er ganz unmittelbar und gewissermassen ganz unvorbelastet der Natur und ihren liebenswertesten Geschöpfen abgelauscht hatte, entweder grundlegende oder doch in jedem Fall höchst wertvolle Beiträge zur Vogelkunde liefern.

Ist das heute noch so? Ich möchte diese Frage keineswegs verneinen, aber im gleichen Atemzug gewisse notwendige Einschränkungen machen. Wie jede Wissenschaft in den letzten 100 Jahren, so hat auch, ja vielleicht in ganz besonderem Masse, die Vogelkunde ihr Haus gewaltig ausgebaut; Tag für Tag wird unermüdlich an der Erweiterung des Gebäudes und an seiner Einrichtung gearbeitet. Die Vorträge dieses Kongresses, die uns über die neuesten Forschungsergebnisse auf Gebieten wie Anatomie, Paläontologie, Systematik, Artbildung, Vogelzug, Verhaltensforschung und Populationsdynamik — um nur einige wichtige zu nennen — einen Überblick vermitteln, beweisen das aufs eindrucksvollste.

Aber noch heute gibt es bei sehr vielen Vogelarten so manche offene Frage, die von einem guten und sorgfältigen Beobachter beantwortet werden kann, und es sind hierbei mit besten Erfolgen Männer und auch Frauen tätig, deren Beruf nicht die Wissenschaft sein kann. Würde man jedoch die Vortragenden der früheren Internationalen Ornithologen-Kongresse mit denen des heutigen im Hinblick auf das zahlenmässige Verhältnis der Berufswissenschaftler zu den „Nichtwissenschaftlern" vergleichen, so ergäbe sich, wie ich meinen möchte, ein abnehmender Anteil der letzteren.

Ist also auch die Ornithologie dabei, mehr und mehr jene Trennung zu vollziehen, die uns in fast allen anderen Wissenschaften nun schon seit langem selbstverständlich ist? Wenn ja, so ist diese Änderung von den Ornithologen weder angestrebt noch verhindert worden, sie liegt vielmehr im Zuge der allgemeinen Wissenschaftsentwicklung.

Andererseits ist die Zahl derer, die sich, ohne Wissenschaftler von Beruf zu sein, doch mit grosser Liebe und Hingabe der Vogelkunde widmen, erfreulich gross; sie ist sogar — wenigstens in Deutschland — seit dem letzten Kriege in besonders starkem Anwachsen. Die Gründe hierfür sind verständlich und auch schon öfters dargelegt, die Auswirkungen bekommen nicht zuletzt die vogelkundlichen Zeitschriften und Institute zu spüren. Diesen starken Zustrom, den unsere scientia amabilis ständig aus jenem Kreise erfährt, in das richtige Bett zu lenken, auch wenn er sich einmal ungebärdig verhält und gar über die Ufer treten möchte, ist eine verantwortungsvolle und nicht immer dankbare Aufgabe der Wissenschaft, also der Museen, der Institute, der fachlichen Vereinigungen, der Schriftleitungen, auch der Volkshochschulen usw. Die deutschen Beringungszentralen zum Beispiel üben sich, wie R. Drost und E. Schüz einmal gesagt haben, geradezu täglich in dieser Kunst. Die Anforderungen, welche die Ornithologie von heute an ihre nichtfachlichen Mitarbeiter stellt, sind ja ganz andere, nämlich höhere und strengere, als noch vor 50 Jahren. Hierfür nur einige Beispiele: Auf Anregung der International Wildfowl Inquiry werden in Nordamerika und in Europa Wasservogel-Bestandsaufnahmen durchgeführt, die bekanntlich ohne den Einsatz von nichtberuflichen Kräften gar nicht durchführbar wären. Für fortpflanzungsbiologische und populationsstatistische Erhebungen bedient man sich in mehreren Ländern der sogenannten Nestkarte, um den nach einheitlichen Gesichtspunkten gesammelten Daten- und Zahlenstoff einer erleichterten Auswertung zugänglich zu machen; jeder Mitarbeitswillige kann solche Vordrucke erhalten. Für vielerlei Fragestellungen wird mehr und mehr die Einzelkennzeichnung vermittels farbiger Ringe oder künstlicher Gefiederfärbung angewendet, da man den Wert und die Erfolgsaussicht dieser Methode erkennt.

Die Frage, ob nun auch an solchen Aufgaben der Vogelfreund, der über kein weiteres Rüstzeug als das einer guten Artenkenntnis verfügt, mitarbeiten und zu ihrer Bewältigung brauchbare Beiträge liefern kann, möchte ich wiederum mit „ja“ beantworten, aber wiederum nicht ohne Einschränkung. So wenig zwei gesunde und geschickte Hände allein schon einen guten Klavierspieler ausmachen, so wenig ist der Vogelartenkenner schon ein Mitarbeiter an ornithologischen Forschungsaufgaben. Es müssen dazu zwei weitere Vorbedingungen erfüllt sein: 1. das Vertrautsein mit dem bereits von anderen Erarbeiteten und mit den derzeitigen Fragestellungen, wozu gute Kenntnis des Schrifttums und laufendes Literaturstudium kaum entbehrlich sind; 2. das Bewusstsein der hohen Verantwortung für jede, auch die scheinbar nebensächlichste Angabe, die der wissenschaftlichen Stoffsamlung beigesteuert wird. Welch hohes Mass von Selbstkritik die letzte Anforderung bedeutet, ist dem Nichtwissenschaftler oft kaum bewusst; denn in fast allen anderen Berufen pflegt es ja als Armutszeugnis zu gelten, wenn jemand von sich bekennen muss: „Das weiss ich nicht“, oder „Das habe ich nicht erfasst“. Hier aber ist es geradezu ein Kriterium der Eignung, ob wir Lücken oder Fehlerquellen oder Unsicherheiten erkennen, sie niemals aus dem Auge lassen und sie, wann immer nötig, offen zugeben.

Einen für die Vogelkunde begeisterten Menschen zum Vogelartenkenner heranzubilden, ist oft kein schweres Stück Arbeit und immer eine Freude. Schwieriger und dabei genau so wichtig ist es, das notwendige Verantwortungsgefühl und die unerlässliche Selbstkritik in ihm zu entwickeln. Wo vogelkundliche Lehrgänge stattfinden, wo ausserhalb des Fachkreises anleitend über Vogelkunde gesprochen oder geschrieben wird, da sollte mehr als bislang hieran gedacht werden. Die Tagebuchnotizen über einen Beobachtungsgang, das Ausfüllen einer Beringungsliste oder Nestkarte, das Aufzeichnen von Beobachtungen an farbig gekennzeichneten Vögeln, all dies und vieles ähnliche erfordet den gleichen wissenschaftlichen Ernst und die gleiche peinliche Sorgfalt wie etwa ein chemisches Versuchsprotokoll, — wenn auch der gemüthafte Anteil daran zu unserer aller Freude um vieles grösser ist!

Ein etwaiger Trennungsstrich soll also durchaus nicht zwischen dem „Fachmann“ und dem „Nichtwissenschaftler“ verlaufen. Vielmehr trennt er diejenigen Vogelkundigen, die sich im Schrifttum auskennen und die verantwortungsbewusst und selbstkritisch zu beobachten und zu berichten gelernt haben, von denen, welche diese Voraussetzungen nicht oder noch nicht erfüllen. Wir wollen bemüht sein, die geeigneten Kräfte aus der letzten Gruppe anzuleiten, damit die erste Gruppe Stärkung und ständigen Zuwachs erfährt. Wo dies nicht angängig ist, oder wo unsere Bemühung auf Unverständnis stossen sollte, da wollen und dürfen wir uns aber auch nicht scheuen, unsere Wissenschaft zu schützen. So wird es gelingen, das hohe Ansehen, welches die Ornithologie unter den Wissenschaften gerade in den letzten Jahrzehnten dank dem Wirken hervorragender Männer sich erkämpft hat, zu erhalten und für die Zukunft zu sichern.

## The Permanent Executive Committee 1950–1954

President: A. Landsborough Thomson, Great Britain, President elect of the XIth Ornithological Congress, Bale 1954.

Members: J. Berlioz, France, J. Delacour, U. S. A., A. Ghigi, Italy, R. Meinertzhagen, Great Britain, E. Stresemann, Germany, A. Wetmore, U. S. A.

Additional Member and Secretary to the Committee: S. Hörstadius, Sweden.

General Secretary to the Congress in Bale 1954; A. Portmann, Switzerland.

## The International Ornithological Committee

(as of June 17, 1950)

| | |
|---|---|
| Argentina | J. Casares |
| Australia | D. L. Serventy |
| Austria | K. Lorenz, M. Sassi |
| Belgium | C. Dupond, R. Verheyen |
| Brasil | O. Pinto |
| Bulgaria | P. Pateff[1] |
| Canada | H. Lloyd, L. L. Snyder |
| Chile | R. A. Philippi B. |
| Colombia | A. Dugand |
| Denmark | B. Løppenthin, K. Paludan, F. Salomonsen |
| Finland | P. Palmgren, I. Välikangas |
| France | J. Berlioz, G. Bouet, E. Bourdelle, P. Engelbach, R. D. Etchécopar, H. Heim de Balsac, M. Legendre, N. Mayaud, G. Olivier, J. Rapine |
| Germany | R. Drost, H. Geyr von Schweppenburg, H. Grote, G. Kramer, O. Koehler, A. Laubmann, W. Meise, B. Rensch, E. Schüz, E. Stresemann, H. Weigold |
| Great Britain | Phyllis Barclay-Smith, D. Bannerman, J. Huxley, N. B. Kinnear, D. Lack, G. Low, R. Meinertzhagen, R. E. Moreau, E. M. Nicholson, A. Landsborough Thomson, W. H. Thorpe, B. W. Tucker, V. C. Wynne-Edwards |

[1] It has later become known that P. Pateff died March 22, 1950.

| | |
|---|---|
| Hungary | A. Keve |
| Iceland | F. Gudmundsson |
| India | Sálim Ali |
| Italy | F. Chigi, A. Ghigi, E. Moltoni, A. Toschi |
| Japan | M. Hachisuka, N. Kuroda, N. Taka-Tsukasa |
| Kenya | J. G. Williams |
| Malaya | C. A. Gibson-Hill |
| Netherlands | L. de Beaufort, P. Hens, H. Kluijver, G. C. A. Junge, G. van Oordt, K. H. Voous |
| New Zealand | R. A. Falla |
| Norway | H. Holgersen |
| Poland | K. A. Wodzicki |
| Russia | G. Dementiev, B. Stegmann, E. V. Kozlova |
| South Africa | J. Vincent |
| Spain | F. Bernis M. |
| Sweden | S. Bergman, N. Gyldenstolpe, G. Rudebeck, G. Svärdson |
| Switzerland | P. Géroudet, H. Noll, A. Portmann, A. Schifferli |
| United States of America | A. A. Allen, W. Beebe, J. P. Chapin, H. Deignan, J. Delacour, H. Friedmann, A. H. Miller, R. C. Murphy, J. L. Peters, A. L. Rand, R. M. de Schauensee, W. E. C. Todd, J. Van Tyne, A. Wetmore |
| Venezuela | W. H. Phelps |

# Règlement des Congrès Ornithologiques Internationaux

*Extrait du Compte Rendu*
*du IX$^{me}$ Congrès Ornithologique International*
*Rouen 1938*

Le Congrès Ornithologique International se réunit tous les quatre ans. Il comprend:

1° Le président et le secrétaire général;
2° Le Comité Ornithologique International;
3° L'ensemble des membres du Congrès.

De plus, le Comité International désigne un Comité Exécutif Permanent composé du président et du secrétaire élus, et de six membres qui demeurent en fonctions pendant quatre ans et sont rééligibles. Le rôle de ce Comité est d'assurer la continuité des travaux et de résoudre les questions qui peuvent se poser entre les sessions du Congrès. Parmi ces six membres, aucune nation ne peut avoir plus d'un représentant.

Le président et le secrétaire du prochain Congrès sont élus par le Comité International; cette élection est notifiée à la séance générale de clôture de la session.

Le Comité International se compose de cent membres, qui conservent leur titre tant qu'ils restent membres du Congrès, à moins qu'ils ne démissionnent volontairement. Le nombre de membres, pour chaque nation, est en rapport avec son activité ornithologique.

Les membres ordinaires du Congrès sont tous ceux qui se sont fait inscrire et ont payé leur souscription.

Le Comité Exécutif Permanent est reconstitué par le Comité International à la fin de chaque session. Il s'entend avec les groupements ornithologiques locaux pour former un Comité Exécutif Local dans le pays choisi pour la réunion du Congrès.

Ce Comité Exécutif Local décide la date et le lieu de réunion du Congrès. Il est responsable de l'organisation locale. Le choix des communications et leur distribution parmi les différentes sections sont laissés à son appréciation.

Le Comité International se réunit une première fois immédiatement avant l'ouverture du Congrés pour combler les vacances qui ont pu se produire par décès, absences ou démissions, et recevoir des suggestions et des invitations pour le Congrès suivant. Une seconde réunion a lieu avant la séance générale de clôture, pour désigner les nouveaux président et secrétaire et choisir le pays où se tiendra le prochain Congrès; s'il existe encore des vacances, elles pourront alors être comblées.

Les décisions du Comité International sont portées à la connaissance du Congrès.

Les membres ordinaires paient une cotisation de 1 livre sterling, ou son équivalent; le montant est utilisé au paiement des frais du Congrès. Le Comité Exécutif Local est chargé de la publication des comptes rendus des travaux du Congrès; toute somme restant disponible par la suite sera versée au Comité Exécutif Permanent.

Tous les membres du Comité International versent, en plus, une contribution de 5 shillings, ou leur équivalent, qui est payable à l'ouverture du Congrès. La somme ainsi produite sert à solder les dépenses préliminaires d'organisation du Comité Exécutif Permanent. Aucun membre ne peut siéger, ni voter, s'il n'a acquitté sa cotisation.

En général, le Congrès se divise en quatre sections: la désignation des présidents de section est faite par le Comité Exécutif Permanent, qui en soumet la liste, pour approbation, au Comité International. Des présidents de remplacement peuvent aussi être nommés.

Ce règlement, approuvé par correspondance en 1932—33 par la majorité des membres du Comité Ornithologique International, a force de loi; mais il est sujet à revision et altérations, le cas échéant, par ce Comité.

**Table of Contents p. 7**

Date Due

~~NOV 7 1960~~
~~APR 19 1961~~
~~MAR 13 1962~~
~~DEC 18 1962~~
~~AUG 27 1963~~
~~NOV 7 1963~~
~~JAN 30 '67~~
~~JAN 10 '68~~
~~JAN 25 '68~~
~~FEB 7 '68~~
~~JUL 1969~~
~~JAN 1974~~
~~JUL 78~~
~~DEC 7 1981~~
~~JUN 30 1983~~
~~APR 23 1987~~

QL671 .I7 1950
Proceedings of the Xth Internationa
Harvard MCZ Library AEJ3793
3 2044 062 342 621

INTER
ORNITH
CONG